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Epitonium (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species

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ABSTRACT

At least six species of the genus *Epitonium sensu lato* are found associated with mushroom corals (Fungiidae) off Ujung Pandang, Sulawesi, Indonesia. Revised descriptions of *E. costulatum* (Kiener, 1838) and *E. ulu* Pilsbry, 1921 based on type specimens and additional material are given. Four new species are described: *E. hoeksemai*, *E. ingridae*, *E. lochi*, and *E. tui-lae*. The true identity of *E. bullatum* (Sowerby, 1844), a species not associated with corals and not found in Sulawesi and nearby areas, is clarified. Examination of type specimens made possible the characterization of nominal species that appear to be either identical with or closely related to the fungiid-associated epitoniids found off Sulawesi.

Key words: Indo-Pacific, parasites, coral reefs, coral/mollusk association, egg capsules.

INTRODUCTION

Several epitoniid species are known to live in association with sea anemones (phylum Cnidaria, order Actiniaria) (Robertson, 1963; 1983a, b; 1993; Vecchio, 1964; Salo, 1977; Perron, 1978; Kay, 1979; Schimek, 1986; Hartog, 1987; Dushane, 1988a–c; Yamashiro, 1990; Nakayama, 1991; Mienis, 1994). Less commonly, epitoniids are found associated with stony corals (phylum Cnidaria, order Scleractinia), in particular with species of the free-living Fungiidae or mushroom corals (Robertson, 1963; 1970; Bosch, 1965; Hadfield, 1976; Kay, 1979; Bratcher, 1982; Loch, 1982; Sabelli and Taviani, 1984; Bell, 1985; Dushane, 1988a–c; Loo and Chou, 1988; Page and Willan, 1988; Hoeksema, 1988; 1989; Yamashiro, 1990; Mienis, 1994; Oliverio *et al.*, 1997). Only three *Epitonium* species are usually mentioned in the literature in association with fungiids; in one case (Loch, 1982) a fourth species is reported but not named. This paper deals mainly with the taxonomy of the surprisingly high number of species of

Epitonium found associated with mushroom corals during a survey in a relatively restricted area in Indonesia, off Ujung Pandang (Sulawesi). Four of these species proved to be new to science, although at least one of them had frequently been cited and illustrated under an incorrect name. The shells of these species are very fragile, which might explain why they are mostly poorly represented or not represented at all in most institutional collections. These species are only known from live-collected specimens: it is very unlikely that empty shells will be found washed ashore without being seriously damaged or unrecognizable. A more elaborate analysis of the ecological data collected during the project is being prepared (Gittenberger, A., unpublished data).

The systematic and evolutionary importance of variable characters such as egg capsules (Figures 36–38), eggs (Figure 41) and mucous threads (Figures 43–47), which can be either straight or twisted, is still poorly known. We observed, however, that populations of the different species may differ in these characters. With exception of one article by Oliverio *et al.* (1997), the literature is scanty in respect to these characters. Oliverio *et al.*, while discussing the coral-associated epitoniid *Epitonium billeanum* Dushane and Bratcher, 1965, figured the egg capsules, eggs, mucous threads (of the twisted type) and shells of veliger larvae. We did not observe a difference in sculpture or well-defined transition between the protoconch 1, formed by the shell gland of the larva inside the egg capsule, and protoconch 2, secreted by the velum of the swimming veliger between hatching and settling. The protoconchs (Figures 16, 25–29, 42, 48) turned out to be very uniform among the various species studied here, all of which apparently have planktotrophic development. Sclerites of at least one species of soft coral, probably of the genus *Simularia* May, 1898 (subclass Octocorallia, order Alcyonacea, family Alcyoniidae) (L. P. van Ofwegen, NNM) were found associated with the egg capsules of some species (Figures 39–40).

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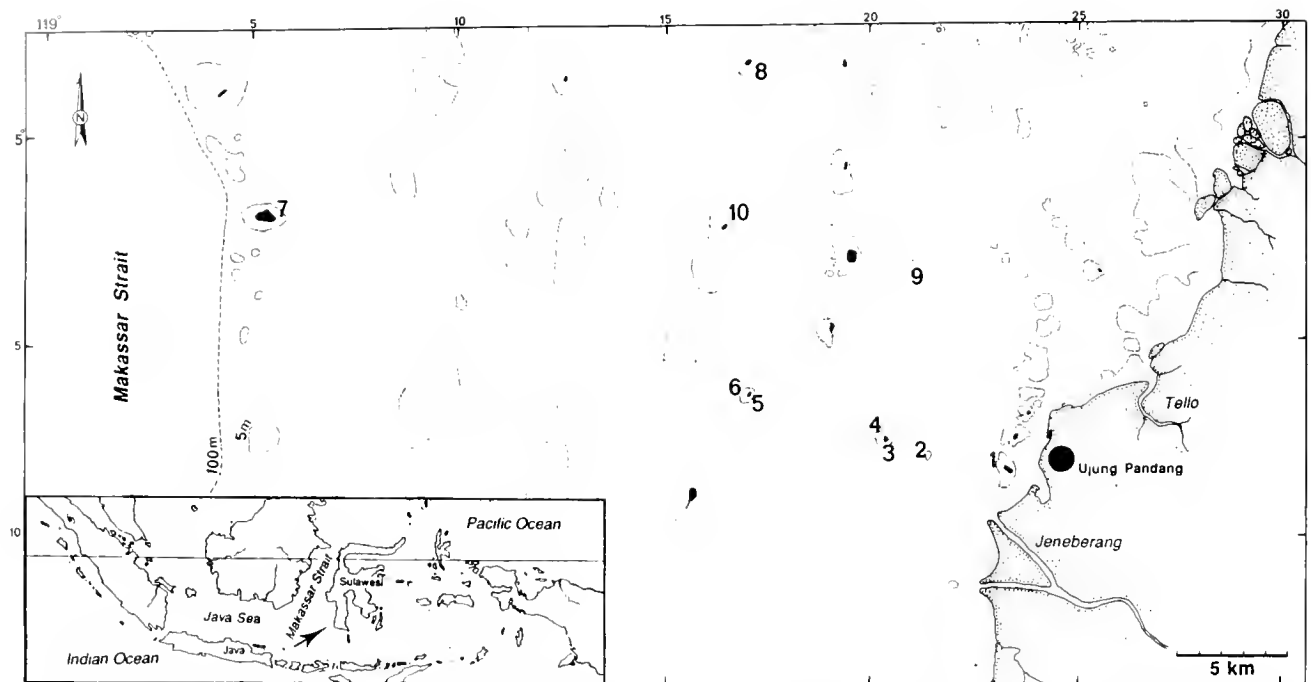


Figure 1. Surveyed area off Ujung Pandang, S. Sulawesi, Indonesia. The coral reefs investigated in particular are: 1, W (Pulau) Lae-Lae; 2, W Bone Baku; 3, E (Pulau) Samalona; 4, W (Pulau) Samalona; 5, E and ESE (Pulau) Kudingareng Keke; 6, W (Pulau) Kudingareng Keke; 7, NW Lan[g]kai; 8, Pulau Badi; 9, Bone Lola; 10, (Pulau) Bone Tambing.

In a monograph on Epitoniidae from southern Africa and Mozambique, Kilburn (1985: 240) stated that "epitoniid taxonomy remains in a chaotic state, particularly above the species level." Kilburn observed that the classification of the genus *Epitonium* is (p. 280) "very tentative and is aimed solely at grouping together similar species for convenience sake." Clench and Turner (1951) and Bouchet and Warén (1986) followed a similar approach in their revision of eastern Atlantic Epitoniidae. Because we could not unequivocally classify all Indonesian species within one or more of the 19 subgenera used by Kilburn (1985) or the 39 subgenera listed by Wenz (1940) under "*Scala*" (= *Epitonium*), we decided to refrain from following any subgeneric classification.

The epitoniid species described in this study live associated with mushroom corals and at least some of them are so similar that they seem to be closely related phylogenetically. They point to possible adaptive radiation within a single clade. Adequate phylogenetic analyses including other species of *Epitonium* co-occurring with different hosts in the same general area could help clarify whether these species found in association with fungiid corals form a monophyletic group.

MATERIALS AND METHODS

Samples were collected off the coast of Ujung Pandang, Sulawesi, Indonesia. The fungiid fauna of the area (Figure 1) is relatively well known; see Hoeksema (1989) for details. During the period April–June, 1997, 9 coral reefs

were inspected, to a depth of 18 (rarely 24) meters. Approximately 10^4 mushroom corals, belonging to about 30 species of free-living Fungiidae, were searched for epitoniids and their eggs. Beneath these corals, about 10^3 specimens of *Epitonium*, some of which with egg capsules, were collected. The identifications of the coral species were made or at least checked by Dr. B. W. Hoeksema. The snails were classified into morphological categories according to characters of shell, egg capsules, and proboscis. Secondly, the species thus distinguished were analyzed ecologically for preferential depths, hosts, and substrates. The ecological data will be discussed in a future article (Gittenberger, A., unpublished data).

The various *Epitonium* species recorded during the survey were identified by review of the literature, consultation with specialists, and by comparison with material deposited in several collections; this includes comparison with type specimens of conchologically similar taxa. These types are mentioned in the systematic treatment of each species.

From the about 10^3 specimens collected, only shells with more than 4 mm length were measured. The number of specimens (n) measured in the calculation of mean values is mentioned at the beginning of the descriptions. Means are indicated between the extremes (minimum–mean–maximum). To allow for better comparisons, shell sculpture is described for both the fifth teleoconch whorl and where the teleoconch is 5 mm in width, a part of the spire that is in part independent of

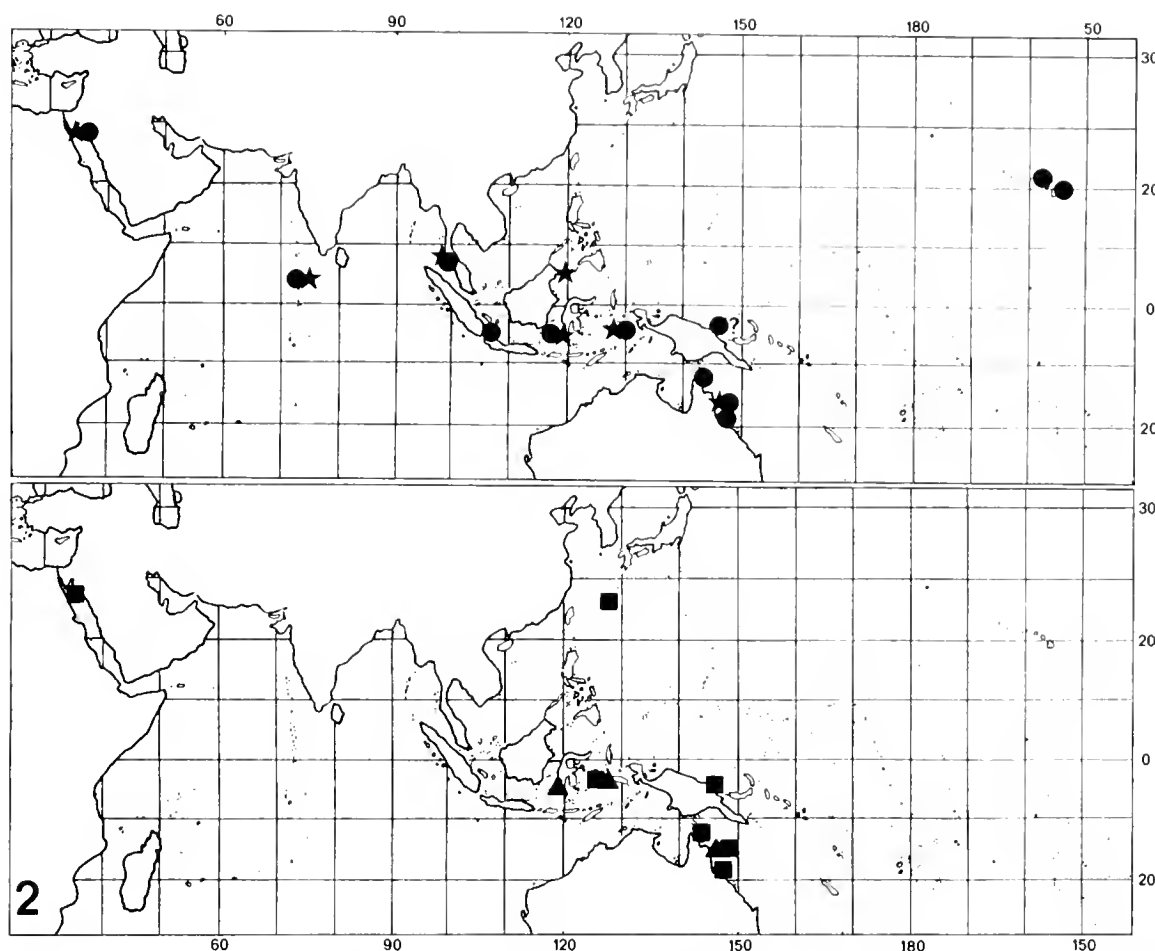


Figure 2. Maps of the Indo-Pacific Region, from the Red Sea to the Hawaiian Archipelago, showing records of the *Epitonium* species in this study known from more than two localities: *Epitonium costulatum* (Kiener, 1838) (stars), *E. ingradae* new species (triangles), *E. twilae* new species (squares) and *E. ulu* Pilsbry, 1921 (circles).

the actual whorl number. The term protoconch refers to the protoconchs 1 + 2. The maximum diameter of protoconch 1 was measured in two shells for each species (except for *E. lochi* because of insufficient material), using SEM photographs of specimens prepared from egg capsules (Figures 30–31); because very similar values were consistently found, no more measurements were taken. Shells of *Epitonium* species cannot be recognized as fully grown or not. Comparative informal observations indicate that when the snails start laying eggs they have not yet reached maximum size. No minimum values are included in the descriptions but only the largest specimen and the largest number of whorls. After removal from 70% ethanol, egg capsules without embedded sand quickly collapsed; these could not be photographed. Unless stated otherwise, all descriptions refer to material from off Ujung Pandang.

The following institutional abbreviations are used: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; LACM, Natural History Mu-

seum of Los Angeles County, Los Angeles; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum national d'Histoire naturelle, Paris; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; NNM, National Museum of Natural History, Leiden. Numbers following a slash sign after collection numbers refer to number of shells in relevant lots.

SYSTEMATICS

Family Epitoniidae Berry, 1910

Genus *Epitonium* Röding, 1798

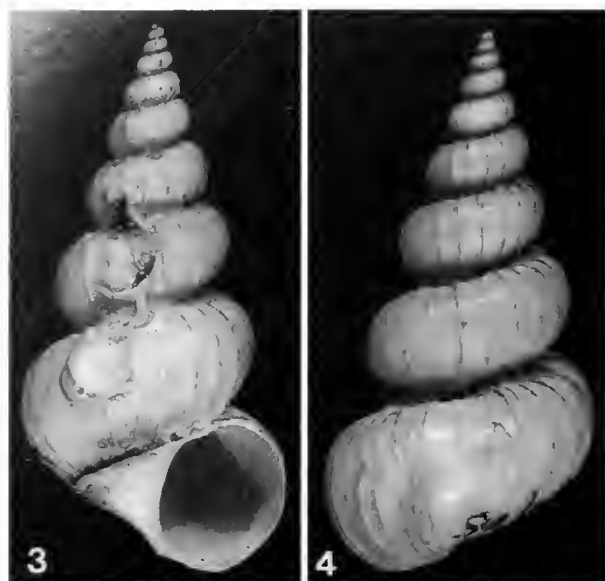
Epitonium costulatum (Kiener, 1838)

(Figures 2–6, 22, 25, 38–41, 47)

Scaloria costulatum Kiener, 1838: pl. 2, fig. 4; 1838: 5.

Epitonium costulatum.—Robertson, 1963: 57, pl. 5, fig. 4; 1970: 45; Loch, 1982: 4, 1 fig.; Dushane, 1988a: 30, figs. 1, 2.

Description: Shell (Figures 3–6, 22, 25) ($n = 7$): Fragile (large specimens) to very fragile, moderately elongate-



Figures 3–4. *Epitonium costulatum* (Kiener, 1838), holotype (MHNG 1152/16). Shell length 3.3 cm.

conical, creamy white, reaching 32 mm in length, with at least 1 damaged specimen (from Ambon) measuring 41.2 mm. Length/width 1.6–1.9–2.2. Protoconch whorls 3 3/8; maximum protoconch 1 diameter 0.14 mm ($n = 2$). Protoconch with numerous fine, incised, axial lines. Teleoconch whorls up to 10, separated by very deep (fenestrate) suture. Successive whorls are almost detached. Teleoconch with evenly spaced, orthocline, thin costae, damaged in all examined specimens. Over most of their length, costae appear to be curved abaperturally at outer margin. Costae adapically relatively high and erect, not coronate, becoming short toward columella. Costae mostly continuous, but touching only slightly those of adjoining whorls. Very weak spiral lines present. Fifth teleoconch whorl (width 4.9 mm) with 16–18.4–26 costae. Five mm width whorl (whorl 4, 5, or 6) with 16–17.4–20 costae. Aperture subcircular. Apertural length/shell length 0.3. Umbilicus moderately wide.

Egg capsules (Figures 38, 39, 40, 47): Embedded with sand and closely connected along a straight, longitudinally striated, mucous thread (Figure 47). Capsules asymmetrical, somewhat conical with a circular widest part. Capsules 3.0–3.3–3.5 mm in length and 1.5–1.6–2.0 mm in width ($n = 8$). One egg capsule contains 70–175–335 eggs ($n = 5$).

Proboscis: With some irregularly interrupted, longitudinal, white zones, which are as wide as transparent interspaces.

Type material (Figures 3–4): Holotype MHNG 1152/16.

Type locality: Unknown.

Other material examined: NNM, Indonesia, Ambon, Hitu, outer part of Ambon Bay, E and W sides of

Laha, A. Fortuin and J. C. den Hartog leg.; LACM 124505, Thailand, Phuket Island.

Records in the literature: Australia: Queensland, Thetford Reef off Cairns (Loch, 1982: 4). Philippines: Bongao Channel, Sanga Sanga (Robertson, 1963: 57–58, pl. 5, fig. 4). Thailand: Raya Island (Dushane, 1988a: 32). Maldives, Little Hiva (Dushane, 1988a: 32). Red Sea: Straits of Tiran (Dushane, 1988a: 30–31); Sinai, Thomas Reef, 27°59'N, 34°27'E (Dushane, 1988a: 32).

Distribution (Figure 2): Australia (Queensland), Indonesia (Sulawesi), Philippines, Thailand, and Red Sea.

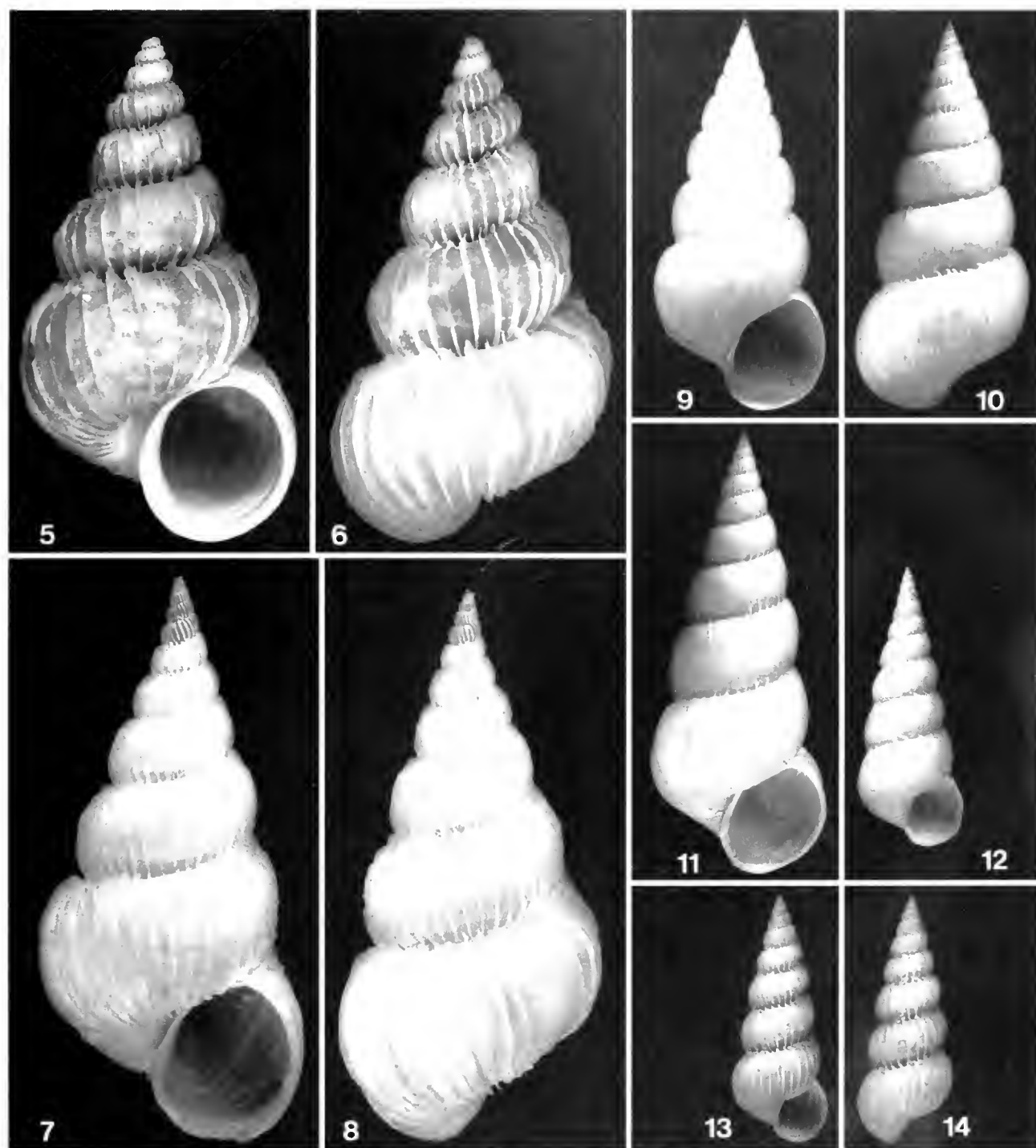
Habitat: Snails were recorded at 6–12 m depth. Coral hosts were *Ctenactis echinata* (Pallas, 1766), and *Herpolitha limax* (Esper, 1797). Groups of one to four snails were found in the sand (sometimes buried) under a single coral; sometimes close to a few hundred egg capsules.

Remarks: The data provided by Sherborn and Woodward (1901) are insufficient to indicate the exact year of publication of the new taxa in Kiener's monograph on the 'Genre Scalaire'. We follow Troschel (1839), who listed Kiener's undated work, with the new species in it, in his 'Report on the achievements in zoology during the year 1838. V. Mollusca' [in German]. The names are printed both on the plates and in the main text of Kiener's work. The severely damaged holotype of this species (Figures 3–4) is a relatively elongate shell. Shells of this species are most similar to those of *Epitonium pallasii* (Kiener, 1838), a species originally described from an unknown locality, but now known from the Indo-West Pacific (Kaicher, 1980: 2382; Eisenberg, 1981: pl. 37, fig. 9; Wilson, 1993: 278, pl. 44, fig. 6a–b). According to Kiener (1838) and in agreement with Wilson's description ("about ten costae on the last whorl") and the figures in the literature, *E. pallasii* differs from *E. costulatum* by the stronger shells with thicker costae, which are more widely spaced. Dushane (1988a: 30, fig. 2) figured very similar egg capsules of this species, reporting two connecting threads for material from the Red Sea.

Epitonium hoeksemai A. Gittenberger and Goud new species (Figures 9–10, 18, 20, 26, 43)

Description: *Shell (Figures 9–10, 18, 20, 26) (n = 9):*

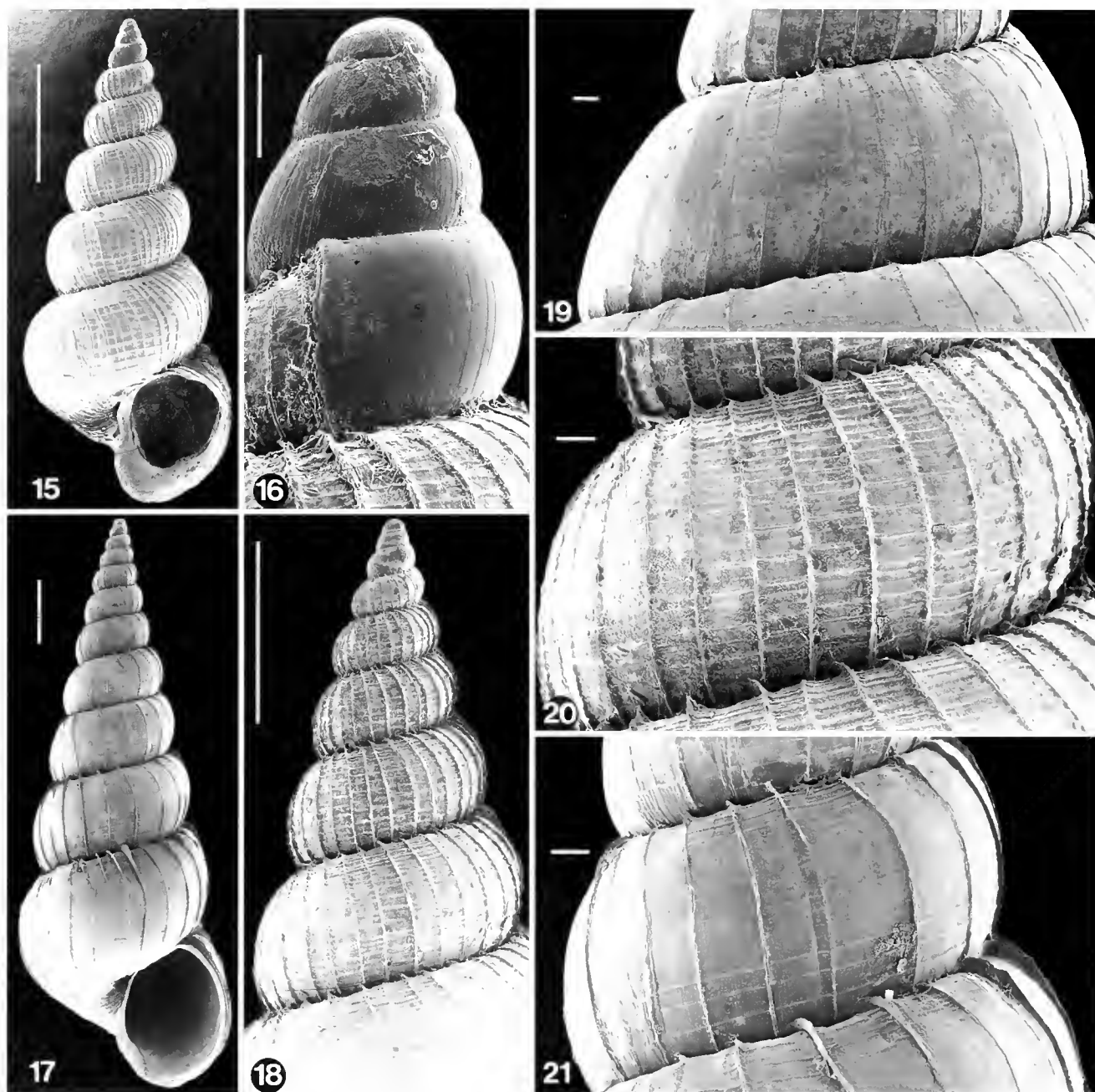
Very fragile, elongate-conical, creamy white, reaching 19 mm in length. Length/width 1.6–1.9–2.4. Protoconch whorls 3. Maximum protoconch 1 diameter 0.13 mm ($n = 2$). Protoconch with numerous very fine, incised, axial lines. Teleoconch whorls up to 9 1/8, separated by a moderately deep suture. Teleoconch sculpture (Figures 18, 20) of somewhat unevenly spaced, orthocline, relatively low costae, and low spiral threads that become conspicuously more numerous and variable on the abapical whorls. Costae on entire teleoconch more prominent than spiral sculpture. Third teleoconch whorl has ca. 12 spiral threads, fifth ca. 25. Costae not always continuous, touching the adjoining whorls, where they are curved adaperturally. Fifth teleoconch whorl (width 2.1



Figures 5–14. Species of *Epitonium* associated with mushroom corals off Ujung Pandang: **5–6.** *E. costulatum* (Kiener, 1838), length 2.8 cm. **7–8.** *E. ingradae* new species, holotype, NNM 59058, length 2.0 cm. **9–10.** *E. hockemai* new species, holotype, NNM 59074, length 1.3 cm. **11–12.** *E. ulu* Pilsbry, 1921, length 1.6 cm and 1.0 cm, respectively. **13–14.** *E. lochi* new species, holotype, NNM 59094, length 0.9 cm.

mm) with 24–27–29 costae. Five mm width whorl (whorl 8, 9 or 10) with 32–35–38 costae. Aperture subcircular. Apertural length/shell length 0.28–0.29–0.30. Umbilicus very narrow.

Egg capsules (Figure 13)—Sub-spherical, white, transparent, with protuberances, no noticeable embedded sand. Capsules closely connected to each other along a twisted mucous thread.



Figures 15–21. SEM micrographs of species of *Epitonium* associated with mushroom corals off Ujung Pandang. **15–16.** *E. lochi* new species **15.** Shell. Scale line = 1 mm. **16.** Protoconch. Scale line = 0.1 mm. **17.** *E. ulu* Pilsbry, 1921, shell. Scale line = 1 mm. **18.** *E. hocksenmai* new species, apical whorls. Scale line = 1 mm. **19.** *E. twilae* new species, teleoconch whorl sculpture. Scale line = 0.1 mm. **20.** *E. hocksenmai* new species, teleoconch sculpture. Scale line = 0.1 mm. **21.** *E. ulu* Pilsbry, 1921, teleoconch whorl sculpture. Scale line = 0.1 mm.

Habitat: This species was recorded between 5–15 meters depth. Coral hosts were *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and *Fungia fungites* (Linnaeus, 1758). One to 5 specimens were found attached by mucous threads to the underside of a coral, near a few hundred egg capsules.

Type material: Holotype NNM 59074, from type locality. Paratypes: NNM 59081/1, Indonesia, Sulawesi, off Ujung Pandang, W. Lae-Lae, 9 m; NNM 59079/1, MZB/1, W. Bone Baku, 6 m; NNM 59080/1, 59082/1, 9 m; NNM 59086/2, type locality; NNM 59076/1, 6 m; NNM 59077/5, 12 m; NNM 59083/1, E. Kudingareng Keke, 3

m; NNM 59078/1, W. Kudingareng Keke, 12 m; NNM 59075/1, 14 m; NNM 59084/1, NW. Lankai, 6 m; NNM 59087/2, Bone Lola, 15 m; NNM 59085/1, Bone Tambung, 6 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W Samalona, 5 m depth.

Distribution: Only known from Indonesia, off Sulawesi.

Etymology: This species is named after Dr. B. W. Hoeksema, who supervised the field portion of this project.

Remarks: Shells of this species resemble those of *Epitonium ulu*, but differ by a length/width ratio of ca. 1.9 instead of ca. 2.6. Because most examined specimens are damaged, the fine structure of the costae could not be observed. The teleoconch sculpture appears always obsolete to the naked eye and the number of spiral threads increases more evidently in *E. hoeksemai*, with ca. 13 spiral threads added between the third and the whorl. In *E. lochi* new species (see below), on the other hand, there is a more clearly reticulate sculpture on the early teleoconch whorls.

Epitonium ingridae A. Gittenberger and Goud new species (Figures 2, 7–8, 23–24, 27, 30, 36, 46)

Description: Shell (Figures 7–8, 23–24, 27, 30) ($n = 5$): Very fragile, moderately slender conical, creamy white; reaching 20.8 in length. Length/width 2.0–2.2–2.3. Protoconch whorls ca. 3. Protoconch with three whorls, with numerous fine, incised, axial lines. Maximum diameter of protoconch 1, 0.14–0.15 mm ($n = 2$) (Figure 30). Teleoconch whorls up to 10, separated by deep suture. Teleoconch sculpture of evenly spaced, orthocline, thin, lamellate costae, and numerous very fine spiral threads (>100 on the 9th whorl), superimposed on somewhat coarser spiral cordlets (ca. 15 on fifth teleoconch whorl). Initial whorls with multiple, lamellate costae, fused together to form thicker ones (Figures 23, 24). Coarser spiral cordlets are most prominent on initial teleoconch whorls, where they are superimposed on costae (Figure 24); coarser cordlets become obsolete on most abapical whorls. Costae are more or less damaged in all specimens; better preserved costae coronate. Particularly below the periphery, costae somewhat curved abaperturally at their free margins, whereas adapically more erect and slightly curved abaperturally or adaperturally near suture, depending on position of costa on adjoining whorl. Costae mostly continuous, but hardly touching each other. Fifth teleoconch whorl (width 3.8 mm) with 20–24–31 costae. Five mm width whorl (whorl 6 or 7) with 23–30–33 costae. Aperture subcircular. Apertural length/shell length 0.3. Umbilicus very narrow.

Egg capsules (Figures 36, 46) ($n = 8$): Oval (Figure 36), embedded with sand and closely connected along straight, longitudinally striated, mucous thread (Figure 46). Capsules 3.0–3.3–3.5 mm length and 1.5–1.6–2.0 mm in width. Capsules contain 93–120–173 white eggs.

Proboscis: Whitish.

Type material: Holotype NNM 59088, from type locality. Paratypes: NNM 59089/1, Indonesia, Sulawesi, off Ujung Pandang, W. Kudingareng Keke, 12 m; NNM 59090/2, 59092/1, E Samalona, 9 m; NNM 59091/1, 24 m; NNM 59093/1, Bone Tambung, 7 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, ESE. Kudingareng Keke, 15 m.

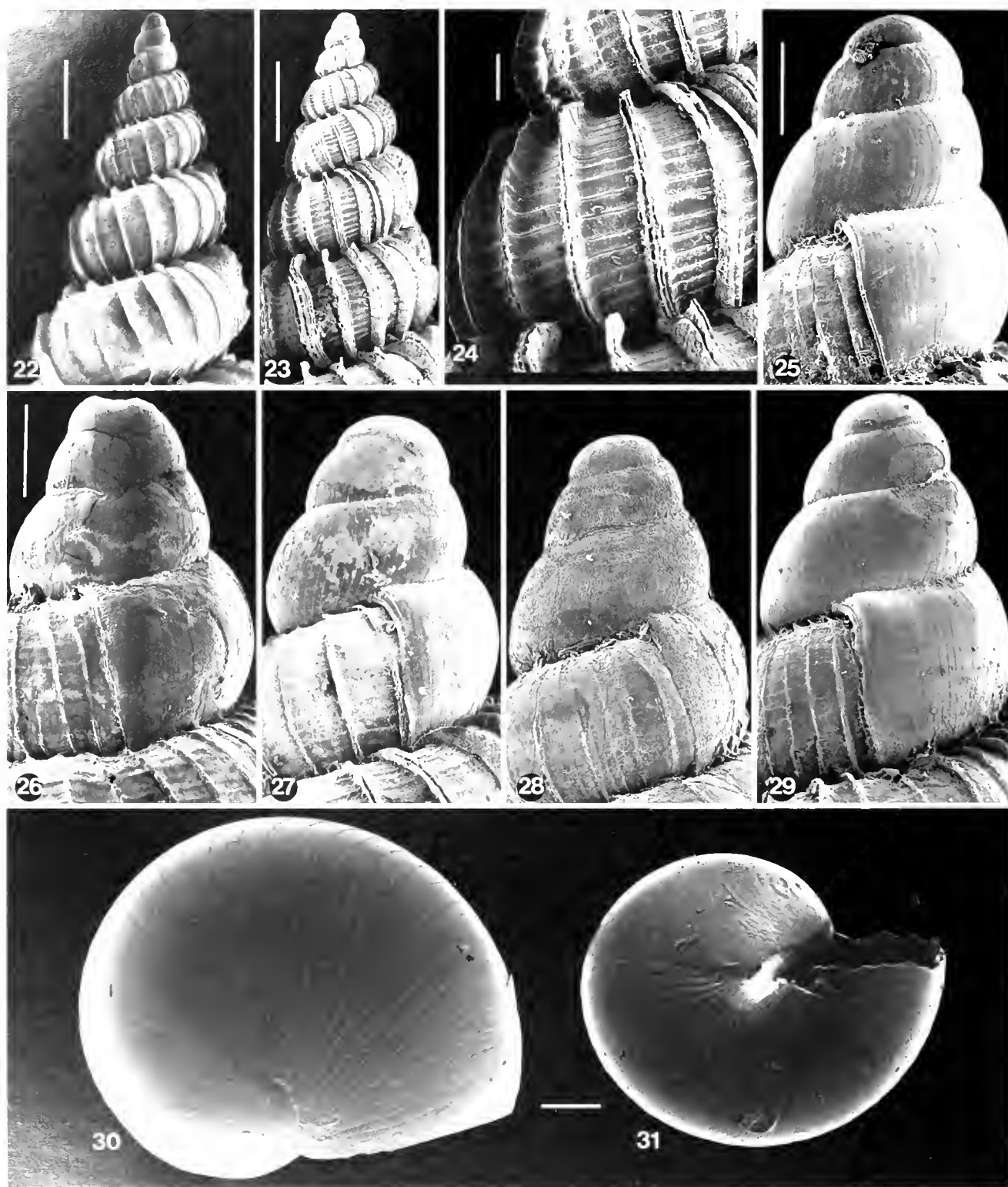
Other material examined: AMS 329657, Australia, Queensland, off Macgillivray Bay, Lizard Island, 14°39'S, 145°29'E, 10 m, 1. Loch leg.; NNM unnumbered, 1 shell, Indonesia, Ambon, Hitu, outer part of Ambon Bay, eastern Laha, J. C. den Hartog leg.

Distribution (Figure 2): Australia, Queensland; Indonesia, Ambon, and Sulawesi.

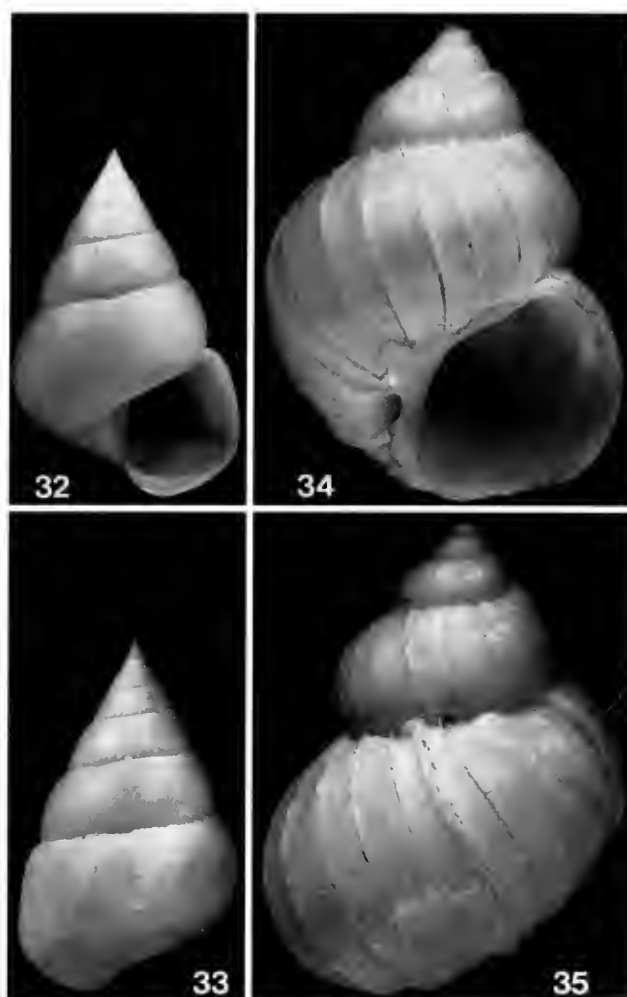
Habitat: Specimens of this species were found between 7–24 meters depth. Coral hosts were *Fungia concinna* Verrill, 1864, *F. fungites*, *Heliofungia actiniformis*, *Herpolitha limax* and *Polyphyllia talpina* (Lamarck, 1801). Specimens were found attached by mucous threads to the underside of a coral; one or two specimens were found associated with up to a few hundred egg capsules.

Etymology: This species is named after Ms. Ingrid van der Loo, Leiden.

Remarks: Conchologically this species resembles the 'probable holotype' (Kaicher, 1981: 3036) of *Epitonium dubium* Sowerby, 1844 (BMNH 1981234) from the Philippines, which is an imperfect shell with a broken aperture and several apical whorls missing. Its length could have been ca. 20 mm. Costae of adjacent whorls are continuous, slightly curved toward aperture adapically and away from aperture abapically, not projecting over suture. The holotype of *Epitonium dubium* most clearly differs from *E. ingridae* by its less prominent teleoconch sculpture and thicker, not lamellate costae. The specimen figured by De Boury (1912: pl. 7, fig. 4, *Scala dubia*), which might represent *E. dubium* (cf. Kilburn, 1985: 327) has more oblique costae. The identity of *Scaloria grayi* Nyst, 1871, (*nomen novum* for *Scaloria striata* Gray, 1847, not Defrance, 1827) is unclear; Tryon (1887: 60, as *S. striata*) and De Boury (1912: 95, as *S. striata* and *S. grayi*) considered this nominal taxon a synonym of *S. dubia*. Kilburn (1985: 327) questioned this synonymy. The shell of *S. grayi* figured by Tryon (1887: pl. 12, fig. 68, as *S. striata*) has a more shallow suture and relatively larger aperture when compared to *E. ingridae*. The new species also resembles *Epitonium friabilis* (Sowerby, 1844) from Western Australia, Swan River. The holotype (BMNH 1966653), figured by Kaicher (1980: 2329), is 16 mm in length and 7 mm in width, with ten whorls. It differs most conspicuously from *E. ingridae* by its closed umbilicus and absence of spiral threads. The species described and illustrated from Sydney Harbour as *Foliaceiscala barissa* by Iredale (1936:



Figures 22–31. SEM micrographs of species of *Eptenium* associated with mushroom corals off Upung Pandang (unless stated otherwise). 22–25. *E. costulatum* (Kiener, 1838), Indonesia, Ambon, Hitu, outer part of Ambon Bay, W Laha, apical whorls. Scale line = 0.1 mm. 23–24. *E. angulata*, new species. 23. Apical whorls. Scale line = 0.5 mm. 24. Teleoconch whorl sculpture. Scale line = 0.1 mm. 25. *E. costulatum* (Kiener, 1838) (same shells as figure 22). Scale line = 0.1 mm. 26–29. *E. hocksemai*, new species. 26. *E. hocksemai*, new species. 27. *E. hocksemai*, new species. 28. *E. tuluae*, new species. 29. *E. ulu* Pilsbry, 1921. Scale line = 0.1 mm. 30–31. *Eptenium* sp. nov. 30. *Eptenium* sp. nov. 31. *E. tuluae*, new species. Scale line = 0.02 mm.



Figures 32–35. Species of *Epitonium* often confused in the literature. **32–33.** *E. twilae* new species, holotype, NNM 59104, length 1.5 cm. **34–35.** *E. bullatum* (Sowerby, 1844), holotype, BMNH 198136, length 2.0 cm.

300, pl. 22, fig. 15) seems to be similar in shape and size, but the costae are described as “of different strength, some fine, others large and recurved, while still others approach varices in size.”

Epitonium lochi A. Gittenberger and Goud new species (Figures 13–16, 37, 45)

?*Epitonium* species 4: Loch, 1982: 4–5, 1 fig. (see remarks below).

Description: *Shell* (Figures 13–16) ($n = 4$): Very fragile, elongate-conical, creamy white, reaching 8.5 mm in length. Length/width 2.0–2.3–2.7. Protoconch whorls 3.25. Maximum diameter of protoconch 1 diameter 0.12 mm ($n = 1$). Protoconch with numerous fine, incised, axial lines. Teleoconch whorls up to 8, separated by a very deep suture. Teleoconch with evenly spaced, orthocline, lamellate costae, crossing low spiral threads that are approximately a half to a fifth as wide as interspaces (Figure 15). Reticulate pattern present on most adapical whorls, replaced by spiral threads on later

whorls. Third whorl with ca. 13 spiral threads, fifth one with ca. 15; spiral threads equally prominent throughout whorl. Costae usually not continuous, lamellar but rather low, barely touching preceding whorl. Due to damage in most specimens, fine structure of costae could not be examined. Fifth teleoconch whorl (width 1.3 mm) with 24–25–26 costae and 12–13–15 spiral threads. Aperture subcircular. Apertural length/shell length 0.22–0.23. Umbilicus absent.

Egg capsules (Figures 37, 45): The roundish, white, egg capsules (Figure 37) are mixed with sand, and closely connected to each other along a straight mucous thread without well-defined sculpture (Figure 45).

Type material: Holotype NNM 59094, from type locality. Paratypes: NNM 59095/2, 59096/1, Indonesia, Sulawesi, off Ujung Pandang, MZB/1, type locality; 16 m; NNM 59098/1, 18 m; NNM 59099/1, E Kudingareng Keke, 3 m; 59100/1, 12 m; 59102/1, 18 m; NNM 59101/2, ESE Kudingareng Keke, 15 m; 59103/1, Pulau Badi, 24 m. See also Remarks.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W Kudingareng Keke, 12 m.

Other material examined: AMS 329687/2, Australia, Queensland, Lizard Island, Watsons Bay, 14°40'S, 145°27'E, 24 m, I. Loch leg.; AMS 329688/1, 329689/1, Granite Bluff, 14°39'S, 145°27'E, 23 m, I. Loch leg. (see Remarks below).

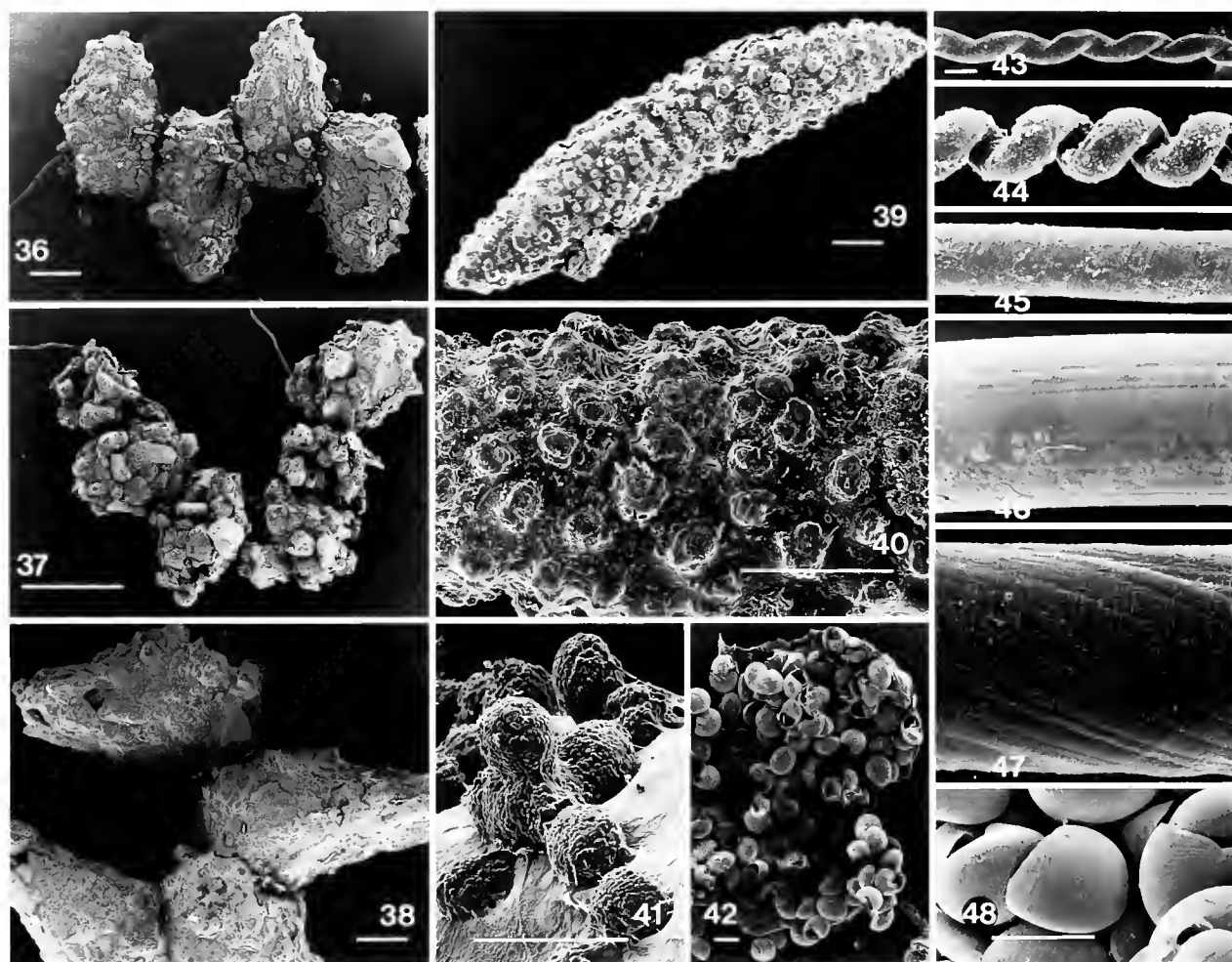
Distribution: Indonesia and probably Australia.

Habitat: The snails were found between 3–24 m. *Fungia costulata* Ortmann, 1889, and *F. tenuis* Dana, 1846, were coral hosts. If the Australian record really proves to be this new species, *Fungia cyclolites* Lamarck, 1816, should be included as an additional host (Loch, 1982: 4). One to 4 specimens were found attached by a straight mucous thread (Figure 45) to the underside of a coral accompanied by up to a few hundred egg capsules.

Etymology: This species is named after Mr. Ian Loch, who described this or a very similar species from Australia, without naming it.

Remarks: Loch (1982) referred to and figured an unnamed ‘species 4’ from Australia, distinguishing it from *E. ulu*. We were able to compare that material with the specimens collected off Ujung Pandang. In the Australian specimens, the spiral threads are somewhat more prominent, which could represent some degree of intra-specific variation. The limited amount of material does not allow for conclusions on the identity of the Australian specimens; this prevented their inclusion as paratypes.

Conchologically this species is most similar to *Epitonium zatrephe* Melvill, 1910 (holotype BMNH 191281683), from the Mekran coast. This shell is figured by Kaicher (1980: 2377); it differs by having continuous



Figures 36–48. Species of *Epitonium* associated with mushroom corals off Ujung Pandang. **36–38.** Egg capsules. **36.** *E. ingradae*. Scale line = 1 mm. **37.** *E. lochi* new species. Scale line = 1 mm. **38.** *E. costulatum* (Kiener, 1838). Scale line = 1 mm. **39.** Sclerite of alcyoniid octocoral found in association with egg capsules of *E. costulatum*. Scale line = 0.1 mm. **40.** Detail of figure 39. Scale line = 0.1 mm. **41.** *E. costulatum*. Eggs within a capsule. **42.** *E. ulu*. Egg capsule with protoconchs 1. Scale line = 0.1 mm. **43–47.** Mucous threads. Scale line, with figure 43, = 0.01 mm. **43.** *E. hocksemai*. **44.** *E. ulu*. **45.** *E. lochi*. **46.** *E. ingradae*. **47.** *E. costulatum*. **48.** *E. twilae*, larval shells (= protoconchs 1). Scale line = 0.1 mm.

costae and by the more narrowly spaced spiral threads, which are about as wide as their interspaces.

The holotype of *Epitonium obliqua* (Sowerby, 1844) [*Scalaria*] (BMNH 1981231) also resembles *E. lochi*, but differs in having a clearly open, though narrow, umbilicus, and continuous costae.

The holotype of *Epitonium deflersi* (Jousseaume, 1911) [*Tenuiscala*] (MNHN De Boury-2706) from Aden, which has a broken aperture and missing apical whorls, can notwithstanding be distinguished from *E. lochi* by the relatively small shell length/width ratio (only ca. 1.9) and the presence of some varices. This holotype is also figured by Kaicher (1981: 3116).

Epitonium twilae A. Gittenberger and Gond new species (Figures 2, 19–25, 32–33, 48)

Epitonium bullatum (Sowerby, 1844): Dushane, 1988: 30, figs. 5, 6. Yamashiro, 1990: 299, figs. 1–6. Not *Scalaria bullatum* Sowerby, 1844

Epitonium species 2: Loch, 1982: 3–4, 1 fig.

Epitonium sp.: Bratcher, 1982: 3, fig. 1.

Description: Shell (Figures 19, 28, 31, 32–33, 48) ($n = 20$): Very fragile, broad-conical, creamy white, reaching 17 mm in length. Length/width 1.2–1.4–1.6. Protoconch whorls 3. Protoconch with numerous very fine, incised, axial lines. Maximum protoconch 1 diameter 0.12–0.13 mm ($n = 2$). Teleoconch whorls up to 9, straight-sided, separated by a shallow suture. Teleoconch sculpture (Figure 19) of unevenly spaced, fine, orthocone, more or less obsolete costae, not or only in part lamellate, and numerous low spiral threads that are separated by interspaces that vary from as wide as the spiral threads to three times as wide. Costae not continuous, not curved, barely touching adjacent whorls. Fifth teleoconch whorl (width = 2.5 mm) with 19–24.4–30 costae. Five mm width whorl (whorl 6 or 7) with 24–31–36 cos-

tae. Aperture subcircular. Apertural length/shell length 0.37–0.44–0.52. Umbilicus very narrow.

Egg capsules ($n = 10$): Egg capsules roundish, white, transparent, with protuberances, without embedded sand, closely connected along straight mucous thread. Egg capsules 1.2–1.4–1.6 mm diameter with 342–425–532 white eggs per capsule.

Type material: Holotype NNM 59104, from type locality. Paratypes: NNM 59149/1, Indonesia, Sulawesi, off Ujung Pandang; W. Lae-Lae, 7 m; NNM 59148/2, 9 m; NNM 59145/1, type locality, 3 m; NNM 59105/1, 59138/3, 6 m; NNM 59127/1, 59129/1, 59141/10, 59147/1, 59150/2, 9 m; NNM 59126/1, 59142/1, 59143/1, 12 m; NNM 59146, 15 m; NNM 59139, ESE Samalona, 5 m; NNM 59131/4, 12 m; NNM 59140/5, 13 m; NNM 59116/1, 59117/1, 59132/3, 59133/2, 59134/1, 59135/1, W Samalona, 9 m; NNM 59121/1, 59122/1, 12 m; NNM 59118/1, 15 m; NNM 59151/1, E Kudingareng Keke, 9 m; NNM 59106/1, 59107/1, W Kudingareng Keke, 9 m; NNM 59115/3, 10 m; NNM 59113/1, 59114/1, 12 m; NNM 59108/1, 59109/1, 59110/1, 59111/2, 59112/1, 15 m; NNM 59123/1, 59124/1, 18 m; NNM 59152/1, 59153/1, 24 m; NNM 59137/1, NW Lankai, 12 m; NNM 59159/5, Pulau Badi, 25 m; NNM 59161/2, Bone Lola, 8 m; NNM 5959160/1, 9 m; NNM 59154/2, 59155/2, 59156/2, 59163/1, Bone Tambung, 5 m; NNM 59157/1, 22 m. Only the specimens from off Ujung Pandang are considered the type series (see Distribution below).

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Bone Baku, 6 m.

Other material examined: AMS 329653/1, Australia, Queensland (see also Loch, 1982: 3, 4, 1 fig.): No. 5 Sandbank Reef, 13°45'S, 144°16'E, 9 m, 1. Loch leg.; AMS 099803/2, 099804/1, 099805/1, 099806/1, 100188/14, 329680/1, 329683/2, off Lizard Island, 14°39'–14°42'S, 145°23'–145°28'E, 2–11 m, P. H. Colman, 1. Loch and W. F. Ponder leg.; AMS 329672/1, Opal Reef, N. of Cairns, 16°15'S, 145°50'E, 9 m, 1. Loch leg.; AMS 096575/2, 101238/2, 147334/2, 329676/4, 329679/3, 329670/1, E–NE of Townsville, 18°46'–18°57'S, 147°31'–147°44'E, 9–18 m, 1. Loch leg. NNM unnumbered, Indonesia, Ambon, Hitu, outer part of Ambon Bay, W Laha, J. C. den Hartog leg.; NNM unnumbered, Sulawesi, off Ujung Pandang.

Records in the literature: Papua New Guinea, Nagada (16 km N of Madang) (Bratcher, 1982: 3, 1 fig.). Japan: Sesoko Island, Okinawa (Yamashiro, 1990: 299–305, figs. 1–6). Red Sea, Sinai, Thomas Reef, 27°59'N, 34°27'E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Australia (Queensland), Papua New Guinea, Indonesia, Japan, and Red Sea.

Habitat: This species was found from 3 m to the maximum diving depth of 24 meters. In the literature that might refer to this species a depth of 45 meters was mentioned (Loch, 1982). The following coral host spe-

cies were recorded: *Ctenactis echinata*, *Herpolitha li-max*, *Saudalolitha dentata* Quelch, 1884, *S. robusta* (Quelch, 1886) and *Zoopilus echinatus* Dana, 1846. Clung with mucous threads to the underside of a coral, one to fourteen specimens were found accompanied by up to a few hundreds of egg capsules.

Etymology: This species is named after Mrs. Twila Bratcher, of Los Angeles, California, USA, who first differentiated the new taxon from *E. bullatum*.

Remarks: This species has been misidentified by various authors (Dushane, 1988a; Yamashiro, 1990; Mienis, 1994, conditionally) as *Epitonium bullatum* (Sowerby, 1844), a species associated with sea anemones (Kilburn and Rippey, 1982; Kilburn, 1985; Mienis, 1994). The badly damaged holotype of *E. bullatum* (Figures 34, 35) has a more globular, far less fragile shell with convex whorls, costae occasionally forming a varix, and only about 5 teleoconch whorls at a length of 19 mm (several apical whorls are missing). The specimens illustrated by Jousseau (1921: pl. 3, fig. 2), Azuma (1962: fig. 2, as *Globiscala kashiwajimensis*), Kilburn and Rippey (1982: pl. 11, fig. 15), Kilburn (1985: 330, figures 160–163) and Wilson (1993: pl. 44, fig. 9) exemplify the variability of *E. bullatum*. Although *E. twilae* differs conspicuously in shape from the other *Epitonium* species in this study, its protoconch (Figures 28, 31, 48) cannot be distinguished from that of these other species.

Yamashiro (1990) published various data on the life history of *E. twilae* (as *E. bullatum*). That author described the egg capsules as elliptical, 0.88 mm in length and 0.75 mm in width, containing 38–98 eggs each. These data differ from our results. Based on very similar shell morphologies, however, we consider his specimens and the ones examined in this section to be conspecific.

Despite the fact that *E. twilae* differs markedly in shell morphology from *E. ulu*, the protoconchs of these species are very similar.

Epitonium ulu Pilsbry, 1921

(Figures 2, 11–12, 17, 21, 29, 44)

Epitonium ulu Pilsbry, 1921: 376, fig. 11c; Bosch, 1965: 267, fig. 1; Robertson, 1970: 45; Hadfield, 1976: 135, Table 1; Taylor, 1977: 253, 255, fig. 7; Kay, 1979: 156, fig. 53a, b; Loch, 1982: 3, 1 fig.; Bell, 1985: 159, figs. 1–6; Dushane, 1988a: 31, figs. 3, 4; 1988c: 9, 1 fig.; Wilson, 1993: 273.

Description: *Shell* (Figures 11–12, 17, 21, 29) ($n = 20$): Very fragile, elongate-conical, creamy white; reaching 16 mm in length. Length/width 2.3–2.6–3.6. Protoconch whorls 3. Maximum protoconch I diameter 0.13 mm ($n = 2$). Protoconch with numerous, very fine, incised, axial lines. Teleoconch whorls up to 12, separated by moderately deep suture. Teleoconch sculpture varying in intensity from well-defined to obsolete. Costae unevenly spaced, orthocline, more or less lamellate or obsolete, not continuous, relatively prominent adapically and clearly encroaching on adjacent whorl, curved in adapertural direction (Figure 21). Spiral threads vary in strength on a single whorl; spiral threads only slightly

increasing in number on later whorls. Fifth teleoconch whorl (width 2.0 mm) with 15–23–28 costae and 9–11–15 spiral threads. Five mm width whorl (between whorl 8 and 11) with 19–28–33 costae and 10–14–25 spiral threads. Aperture circular to somewhat oval. Apertural length/shell length 0.20–0.26–0.29. Umbilicus very narrow to closed.

Egg capsules (Figure 44): Egg capsules roundish to oval, white, granulated, sometimes embedded with sand. Egg capsules closely connected along a twisted mucous thread (Figure 44); Dushane (1988a: 32) reported 3 twisted threads. Capsule diameter 0.8–1.3–1.7 mm ($n = 5$). One capsule contains 67–225–405 eggs. Dushane (1988a: 32) reported 400–600 eggs within a capsule, which she described as papillose, with softly rounded papillae. Kay (1979: fig. 53B) figures the egg capsules as elliptical, 1.1 mm in width and ca. 1.6 mm in length. See Bell (1982; 1985) and Dushane (1988a) for further data on egg capsules, life history, and other relevant data.

Proboscis: Whitish, with some transversal, transparent bands.

Type material: Holotype ANSP 127818, from type locality.

Type locality: USA, Hawaii, Hilo.

Other material examined: ANSP 127818, USA, Hawaii, Big Island, Hilo; AMS 138321/1, Australia, Queensland (see also Loch, 1982: 3, 1 fig.), Eel Reef, 12°24'S, 143°22'E, 4–8 m, I. Loch leg.; AMS 329660/1, Long Sandy Reef, 12°29'S, 143°46'E, 10 m, I. Loch, leg.; AMS 099801/3, 099802/2, 100821/1, 329656/3, near Lizard Island, 14°40'–14°42'S, 145°23'–145°28'E, 1.5–14 m, P. H. Colman and I. Loch leg.; AMS 138320/1, S Escape Reef, 15°53'S, 145°49'E, 18 m, I. Loch, leg.; AMS 096573/7, 329649/2, 329650/1, 329651/1, 329652/1, 329655/2, 329658/7, E–NE of Townsville, 18°46'–18°57'S, 147°31'–147°44'E, 6–15 m, I. Loch leg.; NNM unnumbered, Indonesia: Ambon, Hitu, outer part of Ambon Bay, E and W Laha, A. Fortuin and J. C. den Hartog leg.; LACM 86–163, Java, off Jakarta, Kepulauan Seribu (= Thousand Islands), Pulau Pelangi and Pulau Putri; AMS 138318/1, Malaysia: Pulau Singa Besar, Pulau Langkawi, 6°14'S, 99°44'E, 1 m, I. Loch, leg.

Records in the literature: USA, Hawaii, Oahu, Kaneohe Bay (Bell, 1985: 159–164, figs. 1–6); Papua New Guinea (Dushane, 1988a: 32; Maldives (Dushane, 1988a: 32); Red Sea, Straits of Tiran, Tiran Island and Sinafir Island (Dushane, 1988a: 31, 32, figs. 3, 4); Sinai, Thomas Reef, 27°59'N, 34°27'E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Hawaii, Australia (Queensland), Indonesia, Malaysia, Maldives, and Red Sea.

Habitat: This species was recorded between 3–24 meters depth. Coral hosts were *Fungia spinifer* Clereboudt and Hoeksema, 1987, *F. scabra* Döderlein, 1901, *F. concinna*, *F. horrida* Dana, 1846, *F. scruposa* Klun-

zinger, 1879, *F. fungites*, *F. granulosa* Klunzinger, 1879, *F. scutaria* Lamarck, 1801, *F. moluccensis* Van der Horst, 1919, *F. gravis* Nemenzo, 1955, and *F. paumotensis* Stutchbury, 1833. One to 11 specimens, free or accompanied by up to a few hundreds of egg capsules, were observed on the individual corals, attached with mucous threads to the underside or on the substrate of these hosts.

Remarks: Shells of this species vary considerably in length/width ratio, intensity of teleoconch sculpture and number of costae. They differ from *E. hoeksemai* by a length/width ratio of ca. 2.6 instead of ca. 1.9 and by the presence of less than 20 spiral threads on the fifth teleoconch whorl. It is the most common epitoniid species associated with Fungidae in the study area.

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A new species of *Columbella* (Neogastropoda: Columbelloidea) from the Caribbean Neogene

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ABSTRACT

A new species of *Columbella* is described from the Neogene of the southwestern Caribbean and compared with other Caribbean *Columbella* species. The new species is a member of a species pair differing primarily in inferred larval ecology. Protoconch morphology suggests that the new species had planktic development, whereas its extant analogue, *Columbella mercatoria* (Linnaeus, 1758), has nonplanktic development. Though the 2 species were contemporaneous, they do not appear to have been sympatric.

Key words: Colombia, Costa Rica, larval ecology, protoconch.

INTRODUCTION

Evolutionary divergence in larval ecology between planktic and nonplanktic modes is a common pattern in marine molluscs. Many gastropod genera in several families display both reproductive modes. Recent evolutionary divergence may result in pairs of species differing primarily in larval shell morphology. Traditionally, such variation was considered as evidence for poecilogony, intraspecific variation in larval developmental modes. Recent reviews of poecilogony in marine invertebrates (Hoagland and Robertson, 1988; Bouchet, 1989; Knowlton, 1993; Oliverio, 1996) however, have found little evidence to definitively support that poecilogony occurs. Hoagland and Robertson (1988) reviewed reported cases of poecilogony in marine gastropods, and concluded that the pattern of larval development is generally informative in species-level invertebrate systematics. The purpose of this paper is to describe a new species of columbellid gastropod, *Columbella moienensis*, that differs from another Caribbean *Columbella* species in its inferred developmental mode. Additionally, the 2 species appear to be allopatric, lending further support to their taxonomic distinction.

Columbella Lamarck, 1799 is primarily a tropical American taxon, consisting of 15 Neogene and Recent American species and 2 species in the eastern Atlantic. Phylogenetic analyses of representative columbellid taxa

(deMaintenon, 1999) supports the monophyly of *Columbella*, based on 8 characters of anatomy, radular morphology and shell morphology. Recent species of *Columbella* are differentiated primarily on the basis of conchological characters. The extant species comprise 2 morphological groups, one of which occurs in the Atlantic. The Atlantic *Columbella* species are very similar, and are characterized by having shells with spiral cords over the entire shell surface. They differ primarily in shell coloration and in the number and strength of spiral cords. Jung (1994) recently reviewed the fossil species of the Atlantic group in a discussion of the *Columbella* species from the Neogene of the Dominican Republic. The extant members of the Atlantic group include 2 species in the eastern Atlantic and 2 in the western Atlantic. The known fossil record of the group extends back to the late Miocene. Of the living and fossil species of *Columbella* in the Atlantic, the new species is the only one considered to have planktic development.

The second group comprises the 10 extant Panamic *Columbella* species. These differ from the Atlantic group by lacking spiral cords on the shell except as juveniles. All members of the Pacific group have multiwhorled protoconchs, and are inferred to have planktic development. The fossil record of this group is unknown before the Pliocene, when the extant species appear. Allopatric species pairs differing in developmental mode already have been reported in the group of Atlantic *Columbella* species. Moolenbeek and Hoenselaar (1991) differentiated 2 species in the eastern Atlantic: *Columbella rustica* (Linnaeus, 1758) with nonplanktic development, in the Mediterranean and eastern Atlantic coast, and *Columbella adansoni* (Menke, 1853) with planktic development, endemic to the offshore islands of the eastern Atlantic. Study of allozyme data from these 2 species (Oliverio, 1995, 1996) indicates that they diverged about 2 million years ago. The new species described herein has a similar relationship with one of the western Atlantic species, *Columbella mercatoria* (Linnaeus, 1758).

The following institutional abbreviations are used: UF, University of Florida, Florida Museum of Natural His-

tory; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California Museum of Paleontology; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution.

The micrographs in figures 1 and 2 were taken using the Electroscan Environmental Scanning Electron Microscope at the University of California Museum of Paleontology. Specimens were scanned uncoated, at 15 kV and between 2 and 3 Torr water vapor.

SYSTEMATICS

Family Columbelloidea Swainson, 1840

Genus *Columbella* Lamarck, 1799

Columbella moicensis new species
(Figures 2, 4–8, Table 1)

Description: Shell small, strombiform, up to 19 mm shell length. Aperture length slightly more than half shell length. Protoconch conical, multiwhorled, smooth, with 3 whorls. Teleoconch with 6–7.5 whorls, with spiral cords over all whorls. Body whorl with 12–18 cords counted at the aperture edge, continuing anteriorly to a few finer cords at the base of the shell. Each spire whorl with 4–6 cords visible. Usually with a prominent, slightly nodulose cord at the shoulder, which is most often the second cord below the suture. First 2–3 teleoconch whorls with nodules at the periphery and weak axial ridges, which fade out on subsequent whorls. Aperture constricted by inrolled labial edge, thickest in the center. Labial edge with 10–12 denticles, facing inward. Columella with 2 weak folds. Anterior parietal wall with 5–10 denticles in an axial row. Short posterior parietal callosus, continuous with aperture edge.

Type material: Holotype, UCMP 39918, 12.8 mm long, 7.5 mm wide, type locality. Paratype UCMP 39919, type locality; Paratypes UCMP 39920 and 39921, Upper Tubará Group, below type locality, Punta Pua, Bolívar, Colombia; Paratype USNM 501150, Moín Fm. 2 km west of Puerto Limón, Costa Rica; Paratype USNM 501151, Moín Formation, between Puerto Limón and Pueblo Nuevo, Costa Rica.

Type locality: Upper Tubará Group, Punta Pua, about 15 miles northeast of Cartagena, Bolívar, Colombia (UCMP S-66).

Other material examined: USGS locality 21037, 1 specimen, Moín Formation, outskirts of Puerto Limón, Costa Rica; UCMP S-66, 11 specimens; UCMP S-65, 2 specimens; TU 954, 1 specimen; TU 956, 1 specimen.

Distribution: The known lots of *Columbella moicensis* are from the Pliocene to Pleistocene (?) of Costa Rica and Colombia. The material from Colombia lacks precise stratigraphic data but is thought to be from the Miocene to Pliocene Tubará Group (Vokes, 1990). Vokes (1990) reported that the muricid species she studied

from these 2 Colombian localities are typical of the Pleistocene Moín fauna from Costa Rica. Although the Moín Formation has better stratigraphic definition than the above mentioned units, some controversy exists about the age of the formation. Coates *et al.* (1993) state that the Moín Formation is Late Pliocene in age, however its faunas are more usually considered to be Pleistocene in age (Robinson, 1993, and references therein). Thus the stratigraphic range of this species is currently imprecise.

Etymology: *Columbella moicensis* is named after the Moín Formation of Costa Rica.

Discussion: *Columbella moicensis* is very similar to *Columbella mercatoria* (Linnaeus, 1758) (Figure 3), a common western Atlantic species known from the Pliocene to the Recent. The new species can be differentiated from *C. mercatoria* by its multiwhorled protoconch. *Columbella mercatoria* has 1.5 to 2 bulbous protoconch whorls (Figure 1), with at least one specimen having 2.25 whorls. The new species has a conical protoconch with 3 whorls (Figure 2), and its nuclear whorl is smaller than that of *C. mercatoria*. This latter species has nonplanktic development; its eggs hatch as crawling juveniles after about 33 days, during which the larvae feed on nurse eggs in the capsules (Bandel, 1974). The multiwhorled protoconch of *C. moicensis*, in contrast, is indicative of planktic development.

Columbella mercatoria varies greatly in adult size and strength of sculpturing, as do many other *Columbella* species. In the case of *C. mercatoria*, this variation may be a function of environment. In southern Florida, the species is commonly associated with both reef rock and seagrass habitats, and specimens found in seagrasses tend to be smaller and less brightly patterned than reef specimens. The known specimens of *C. moicensis* come from only 6 lots, and most of the material is similar in size. The single specimen from USGS locality 21037 (USNM 501152, Figure 8) is markedly larger than other specimens (Table 1), and has a weaker shoulder. It does have a multiwhorled protoconch (broken off though still with the shell) consistent with that of *C. moicensis*, so will be referred to the new species in spite of the differences between it and other specimens.

Many of the specimens that are considered to represent *C. moicensis* have eroded protoconchs and thus cannot be diagnosed with certainty. However, they are comparable in shape and size to specimens of *C. moicensis* from the same localities.

Columbella mercatoria was contemporaneous with *C. moicensis*. However, the 2 species have not so far been found sympatrically. *Columbella mercatoria* has been collected in the Pliocene and Pleistocene Mare and Abisinia Formations of Venezuela (Weisbord, 1962) and in the Pliocene Bowden Formation of Jamaica (a worn and damaged specimen incorrectly identified as *Columbella submercatoria* is illustrated by Woodring, 1928).

Columbella submercatoria Olsson, 1922 occurs in the Late Miocene of the Dominican Republic (Jung, 1994)

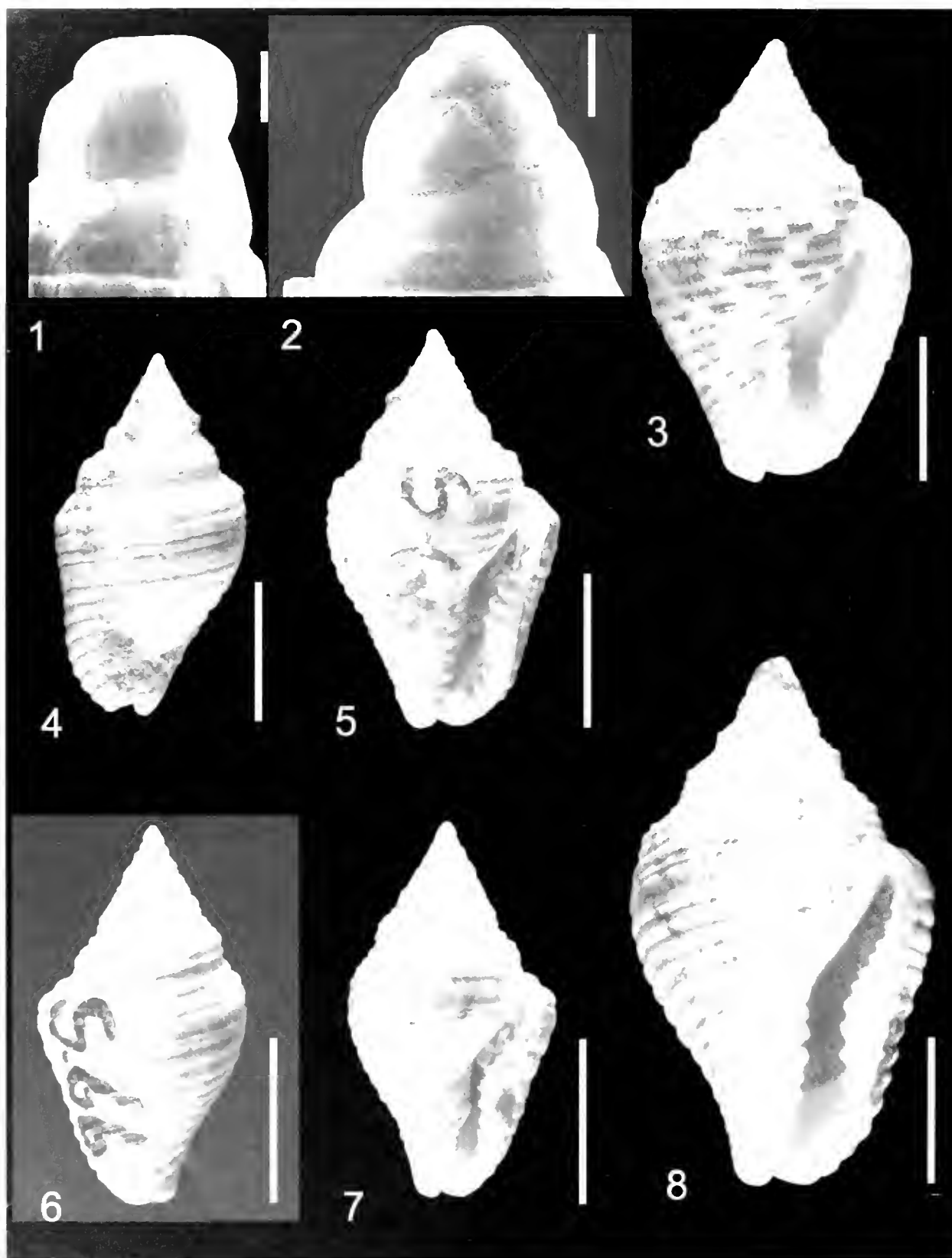


Figure 1. Recent *Columbella mercatoria*, protoconch, UF 126820, Colon Island, Bocas del Toro Province, Panama. Scale line = 200 µm **Figure 2.** *Columbella momensis* new species. Protoconch of paratype, UCMP 39919. Scale line = 200 µm **Figure 3.** Recent *Columbella mercatoria* (SBMNH 144851, Los Totumos, Venezuela). Scale line = 5 mm **Figures 4–5.** *Columbella momensis* new species. Holotype, UCMP 39918. Scale line = 5 mm **Figures 6–7.** *Columbella momensis* new species. Paratype, UCMP 39919. Scale line = 5 mm **Figure 8.** Large specimen of *Columbella momensis* new species, USNM 501152. Scale line = 5 mm

Table 1. Lengths and widths in mm, and number of cords on the body whorl of types and figured specimens.

| Specimen | Max. length (mm) | Max. width (mm) | No. of spiral cords |
|-----------------------|------------------------|--------------------|------------------------|
| Holotype, UCMP 39918 | 12.8 | 7.5 | 14 |
| Paratype, UCMP 39919 | 11.4 | 6.3 | 14 |
| Paratype, UCMP 39920 | 15.3 | 8.7 | 12 |
| Paratype, UCMP 39921 | 15.8 | 9.1 | 17 |
| Paratype, USNM 501150 | 10.1 | 5.5 | 15 |
| Paratype, USNM 501151 | 12.5 | 7.2 | 16 |
| USNM 501152 | 18.6 | 10.4 | 17 |

and in the Neogene of Costa Rica. Whether this is a distinct species or a form of *C. mercatoria* has been debated and should still be regarded as uncertain. The primary difference between them is the greater number of spiral cords on *C. submercatoria* (22 to 25 per whorl rather than 15 to 20), but large specimens of extant *C. mercatoria* from some areas of the Caribbean also have a greater number of spiral cords than usual. The type locality for *C. submercatoria* is Red Cliff Creek, Costa Rica, a locality that is presently unlocated but thought to correspond to late Miocene or early Pliocene beds in the Limon Basin (Jung, 1994). *Columbella submercatoria* has a paucispiral protoconch of about 1.5 whorls (Jung, 1994), similar to that of *C. mercatoria*.

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The New Zealand Recent species of *Muricopsis* Bucquoy, Dautzenberg and Dollfus, 1882 (Gastropoda: Muricidae)

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ABSTRACT

Four New Zealand Recent *Muricopsis* species are recognized: *M. octogonus* (Quoy and Gaimard, 1833), *M. mariae* (Finlay, 1930) and *M. profunda* new species, which belong in subgenus *Murexsul* Iredale, 1915, and *M. scotti* new species, which is referred to *Rolandiella* new subgenus together with the southern Australian species *M. umbilicatus* (Tenison Woods, 1876). Their shells and radulae are illustrated and distributions plotted. *Muricopsis mariae* is interpreted as a species rather than a chronosubspecies of *M. espinosus* (Hutton, 1886) as has been traditional.

Key words: New Zealand, Muricidae, *Muricopsis*, *Murexsul*, new taxa.

INTRODUCTION

For a number of years a large, locally common, sublittoral form of *Muricopsis* from rocky ground off northern New Zealand was suspected to be an unnamed species distinct from *M. octogonus* (Quoy and Gaimard, 1833). Extensive collecting and field observations led Scott (1989) to conclude that distinct species were indeed involved, and he reported differences in shell morphology, operculum colour and habitat. On areas of rocky ground at 12–15 m depth, cut by channels with sand floors, Scott found that whereas *M. octogonus* typically lives both on horizontal rocky surfaces with dominant kelp (*Eklonia radiata*) and on sand at the channel floors, the undescribed species typically lives on the channel walls amongst abundant sponges and brachiopods. The preference for vertical sublittoral rock surfaces would account for its extreme rarity on beaches and in dredge and trawl samples. The following revision was initiated after recent discovery of well preserved juvenile specimens (hitherto unavailable or unrecognised) of the undescribed species, which show additional differences from *M. octogonus* that in turn suggest a closer relationship with the southern Australian species *M. umbilicatus* (Tenison Woods, 1876). Abbreviations and text conven-

tions are: AIM, Auckland Institute and Museum; BMNH, The Natural History Museum, London; CM, Canterbury Museum, Christchurch; IS, Ian Scott collection, Auckland; KWB, Kevin W. Burch collection, Whangarei (includes the outstanding collection formed by our late friend Dave Gibbs); NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; NZGS, Institute of Geological and Nuclear Sciences, Lower Hutt. Unless specified, all material is at NMNZ (registration numbers preceded by "M."). Length dimension precedes width in all cited measurements.

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1815

Family Muricidae Rafinesque, 1815

Subfamily Muricidae Rafinesque, 1815

Genus *Muricopsis* Bucquoy, Dautzenberg and Dollfus, 1882

Muricopsis Bucquoy, Dautzenberg and Dollfus, 1882: 19. Type species (by original designation): *Murex blainvillii* Payraud, 1826; Recent, Mediterranean.

Subgenus *Murexsul* Iredale, 1915

Murexsul Iredale, 1915: 471. Type species (by original designation): *Murex octogonus* Quoy and Gaimard, 1833; Recent, New Zealand.

Remarks: Ponder (1972) considered *Murexsul* to be a synonym of *Muricopsis*, though Radwin and D'Attilio (1976), Vokes (1970, 1988) and Beu and Maxwell (1990) have treated them as distinct genera. We agree with Vokes (1988) that they are closely related, but like Houart (1988, 1991, 1993), prefer to interpret *Murexsul* as a subgenus of *Muricopsis*.

Muricopsis (*Murexsul*) *octogonus* (Quoy and Gaimard, 1833) (Figures 1–15, 24, 25, 33, 37)

Murex octogonus Quoy and Gaimard, 1833: 531, pl. 36, fig. 8, 9; Kiener, 1843: 64, pl. 15, fig. 2; Gray, 1843: 229; Reeve, 1845, pl. 29, fig. 134; Kiister and Kobelt, 1869: 79, pl. 28,

- fig. 23; Hutton, 1880: 47; Poirier, 1883: 112; Suter, 1901: 61.
- Murex peruvianus* Sowerby, 1841a: 8, fig. 103; Sowerby, 1841b: 147; Vokes, 1970: 327. Not *Murex peruvianus* Lamarck, 1816 (preoccupied).
- Murex (Phyllonotus) octogonus*.—Tryon, 1880: 110, pl. 30, fig. 272, 273 only (in part—fig. 274 = *Muricopsis cuspidatus* (Sowerby, 1879)); Hutton, 1884: 218.
- Murex dipsacus*.—Tryon, 1880: 110, pl. 30, fig. 251 only. Not Broderip, 1833.
- Murex octogonus* var. *umbilicatus*.—Suter, 1901: 61. Not Tenison Woods, 1876.
- Murex (Muricantha) octogonus*.—Suter, 1913: 400, pl. 48, fig. 1.
- Murex (Muricantha) octogonus* var. *umbilicatus*.—Suter, 1913: 401. Not Tenison Woods, 1876.
- Hexaplex (Murexsul) octogonus*.—Iredale, 1915: 471; Wenz, 1941: 1090, text fig. 3096.
- Hexaplex (Murexsul) octogonus* var. *umbilicatus*.—Iredale, 1915: 471. Not Tenison Woods, 1876.
- Murexsul octogonus*.—Finlay, 1926: 419; Vokes, 1964: 13, fig. 20, 50, 61; Ponder, 1968: 31, fig. 1, 37–41; Vokes, 1970: 327; Fair, 1976: 63, pl. 17, fig. 239; Radwin and D'Attilio, 1976: 163, text fig. 104, pl. 26, fig. 6, 7; Abbott and Dance, 1983: 143, text fig.; Scott, 1989: 6, text figs.; Ben and Maxwell, 1990: 359, pl. 481.
- Murexsul cucierensis* Finlay, 1926: 419 = *nomen nudum*.
- Murexsul cucierensis* Finlay, 1927: 457, pl. 24, fig. 2.
- Murex (Murexsul) octogonus*.—Thiele, 1929: 290; Shikama and Horikoshi, 1963: 69, text fig. 104.
- Murex (Murexsul) ednae* Smith, 1940: 43, pl. 2, fig. 10.
- Muricopsis octogonus octogonus*.—Ponder, 1972: 237, text fig. 3/24.
- Murexsul octogonus* [sic].—Kaicher, 1978, card 1608.
- Muricopsis octogonus*.—Powell, 1979: 170, pl. 35, fig. 1; Scott, 1989: 6, text figs.; Hart, 1993: 44, text fig. (in part—far right figure = holotype of *M. scotti* new species).

Type material: *M. octogonus*: syntypes (2), including the originally figured specimen (Figure 15) MNHN, Bay of Islands, New Zealand; *M. peruvianus*: repository of type material unknown (not located at BMNH, K.M. Way, pers. comm.), "Pacosmayo, Peru" = New Zealand; *M. cucierensis*: holotype AIM 70500, off Cuvier Island, 73 m; *M. ednae*: repository of type material unknown, "Japan" = New Zealand.

Other material examined: About 1000 specimens in NMNZ (152 lots) and K.W. Burch (24 lots) collections.

Distribution (Figure 37): Pleistocene (Castlecliffian) to Recent. Three Kings Islands and North Island, New Zealand, as far south as Kapiti Island (west coast) and Mahia Peninsula (east coast), 0–508 m; taken alive at low tide to 121 m.

Remarks: *Muricopsis octogonus* is exceptionally variable in teleoconch morphology, and there is complete intergradation between the most extreme of the forms illustrated here (Figures 1–15). Despite great variation in sculpture of the last few whorls in adults, all of the specimens are identical in protoconch and early teleoconch morphology. Moreover, we could detect no differences between the most extreme forms in radular

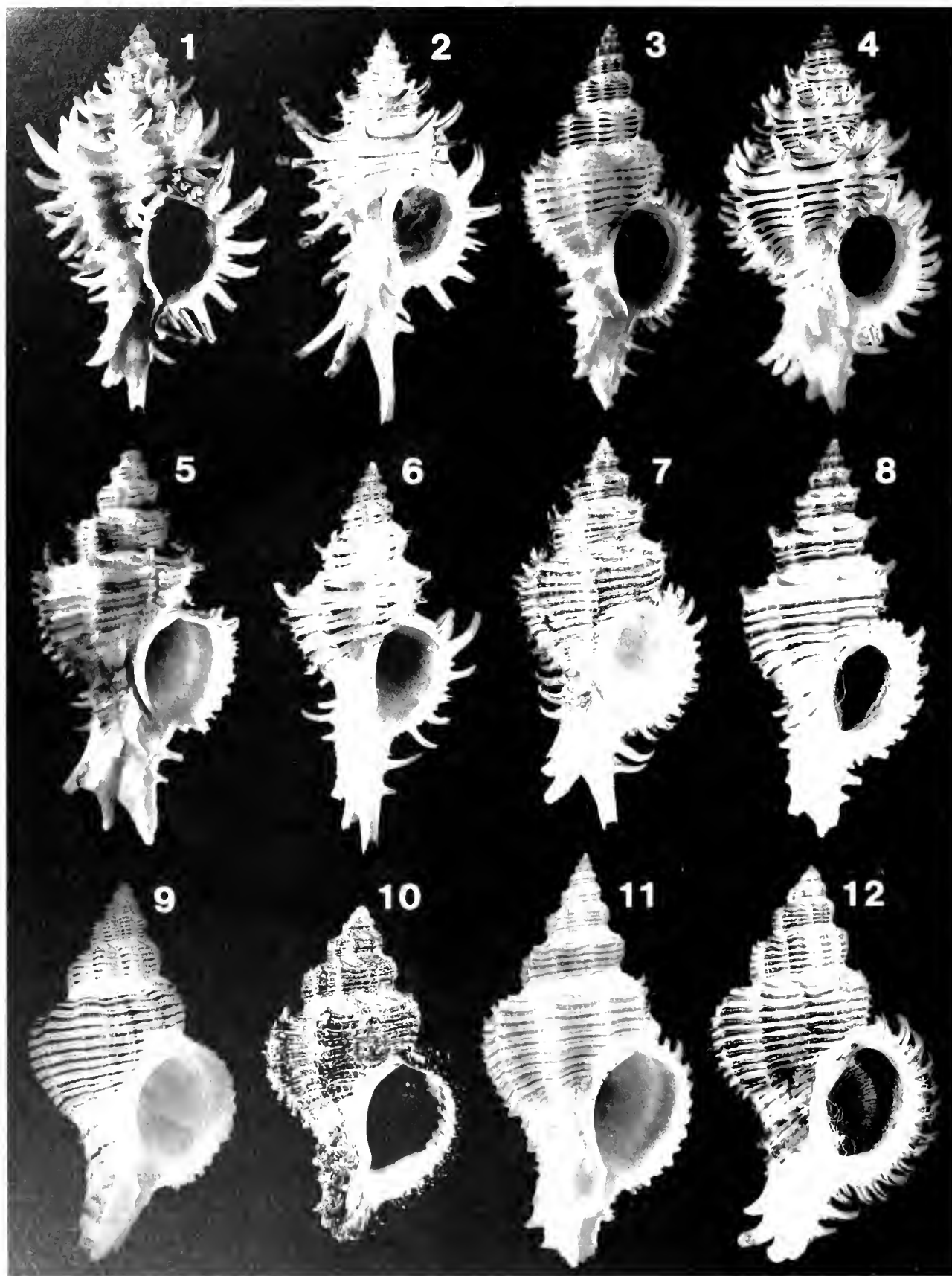
morphology or external anatomy. It thus seems clear that all specimens under consideration here represent a single highly variable species.

Mature specimens range from 29 to 92 (est.) mm in length. Spines may be entirely absent, or short to long. The secondary spiral cords may remain weaker than the primaries and spineless throughout, or they may enlarge to resemble the primaries before the last adult whorl, and some or all may develop spines that may be as long as those on the primaries. The siphonal canal may be short and broad and the fasciole rounded with low ridges, or the canal may be long and narrow, and the fasciole set with canals from earlier stages of growth that encircle a narrow to rather large false umbilicus. The teleoconch may be reddish brown with black spiral cords, or white or cream with yellowish or (typically) reddish brown spiral cords. Shells with dark, extensive pigmentation predominate in the littoral and locally to about 12 m. Specimens with short spines, and with secondary spirals that enlarge to resemble the primaries predominate in the littoral and locally to about 50 m, whereas long-spined shells on which the secondary spirals remain weaker than the primaries typically occur deeper than about 30 m, though locally as shallow as about 20 m. The outer lip of mature specimens may be smooth or (typically) dentate, and the inner lip rim may be free and projecting below a narrow parietal area, or almost fully adherent. Unusually large, entirely spineless shells occur off Spirits Bay, where they intergrade with short-spined specimens (Figures 9, 11).

Muricopsis octogonus has been observed on a number of occasions on sandy substrata, boring holes in and feeding upon the shallowly-burrowing bivalve *Tawera spissa* (Deshayes, 1835) (I. Scott, pers. comm.; K.W.B., pers. obs.). What it eats on rocky ground remains to be established. The radula is illustrated (Figure 33) for comparison with those of *M. mariaae*, *M. scotti* and *M. umbilicatus* (Figures 34–36).

There are no records of *M. octogonus* from the west coast of the North Island between Cape Maria van Diemen and Cape Egmont, or from the east coast south of Mahia Peninsula (Figure 37), and it would seem that the present distribution off the northeastern and southwestern North Island is relictual, perhaps dating from prior to the last glacial maximum.

How far back this species extends in the fossil record is unclear. Specimens from a Late Pliocene (Nukumaruan) horizon near Waipukurau (GS10858, former cutting on disused section of Ashcott Road, coll. A.G. Ben, NZGS) appear to be indistinguishable from Recent specimens in teleoconch morphology, but differ in having smoothly rounded instead of angulate protoconchs as in Recent material (Figure 30) (see below). If it proves to be specifically distinct from *M. octogonus*, it may be assignable to *M. dilucidus* Marwick, 1931 (Early Pliocene, Gisborne District). Some of the New Zealand Cenozoic taxa are scarcely distinguishable from *M. octogonus* or from each other, and it is likely that *M. octogonus* is a direct descendent of one or other of them, such as *M.*



proavitus (Laws, 1935), *M. progenitor* (Laws, 1935), or *M. marwicki* (Maxwell, 1971), all from Middle Miocene (Lilburnian) beds.

Muricopsis (*Murexsul*) *mariae* (Finlay, 1930)
(Figures 17, 19, 27, 28, 34, 38)

Murexsul mariae Finlay, 1930: 237; Kaicher, 1978, card 1639; Ben and Maxwell, 1990: 359.

Murexsul espinosus mariae.—Ponder, 1968: 32, fig. 2, 32, 33, 34.

Muricopsis espinosus mariae.—Powell, 1979: 170, pl. 37, fig. 5; Scott, 1959: 6, text figs.

Type material: Holotype AIM 70502, Cape Maria van Diemen, northern New Zealand.

Other material examined: Several hundred specimens in NMNZ (66 lots) and K.W. Burch (13 lots) collections.

Distribution (Figure 38): Three Kings Islands and northeastern North Island, New Zealand, as far south as Anaura Bay, 0–233 m; taken living under rocks at low tide to 40 m.

Remarks: *Muricopsis mariae* differs principally from *M. octogonus* in consistently lacking spines, in being smaller relative to the number of whorls, in having stronger denticles within the adult outer lip, in attaining smaller size (maximum length 29 mm as against ca. 93 mm), in being bluish white instead of typically white within the aperture, and in typically lacking a distinct shoulder angulation, at least on the early teleoconch whorls (some specimens have a distinct shoulder angulation on later whorls). In a sample of both species taken living together at 25 m in Whangaroa Harbour entrance (M.137244, M.74899), the protoconch ranges from 800–1000 µm wide (mean = 900 µm, SD = 0.053, n = 21) in *M. mariae*, and 650–1050 µm wide (mean = 930 µm, SD = 0.097, n = 17) in *M. octogonus*. The largest *M. mariae* protoconch seen is 1250 µm wide (M.133712). The first whorl of the protoconch has a distinct angulation and the summit is more or less flattened in both species. Juveniles of *M. mariae* and *M. octogonus* may be difficult to distinguish, but in *M. mariae* the primary spiral cords are stronger after the second teleoconch whorl, the secondary spirals enlarge more rapidly to resemble the primaries, and the secondaries on the sutural ramp become pigmented early on the third whorl instead of after the third or fourth whorl (compare Figures 24, 25 with 27, 28). Specimens from Cape Maria van

Diemen to North Cape and off the Three Kings Islands are more broadly conical than most specimens from further south (Figures 17, 19) but are otherwise indistinguishable.

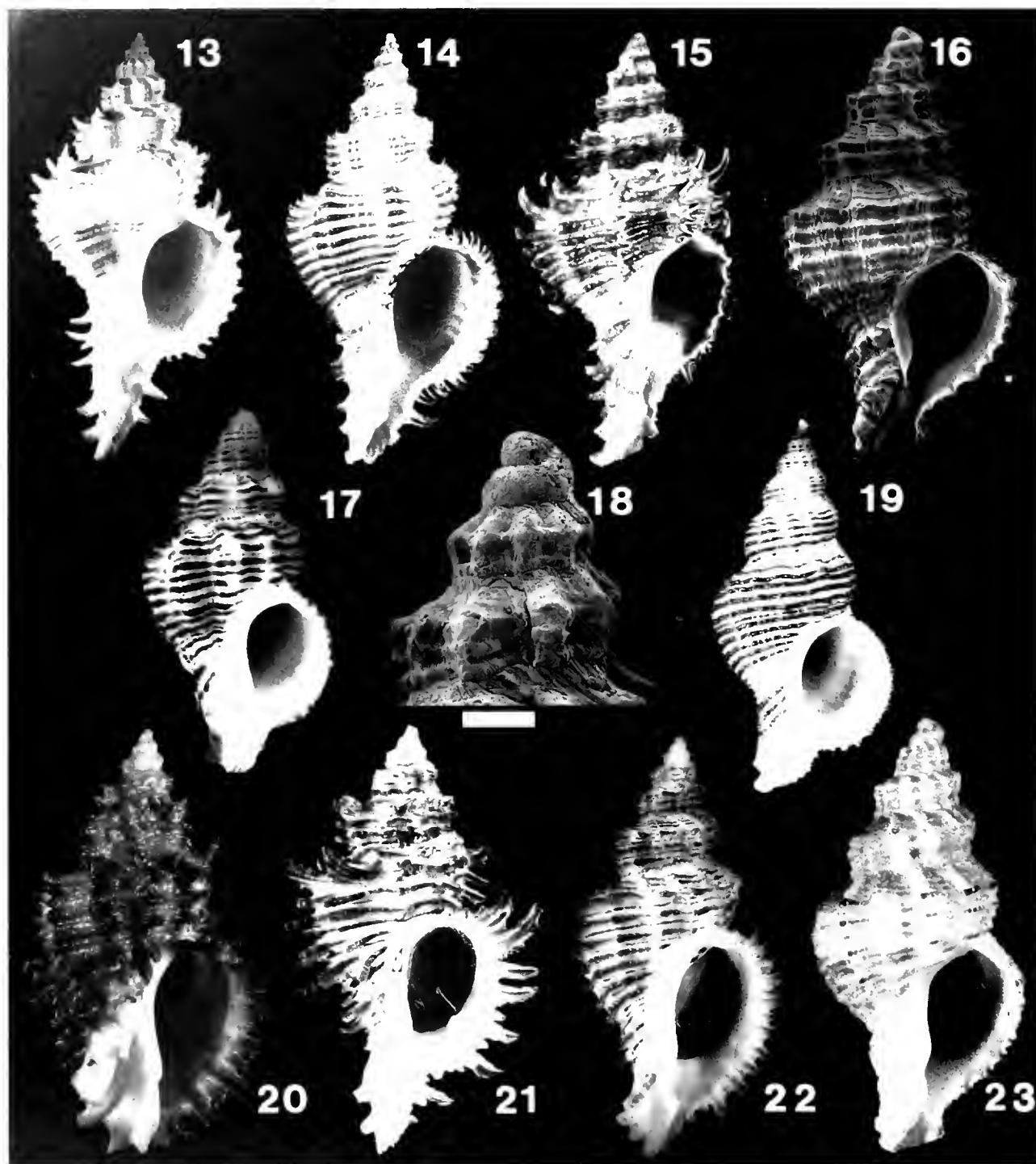
The diet of this species is unknown. The distinctive radula is illustrated (Figure 34) for comparison with that of *M. octogonus*, *M. scotti* and *M. umbilicatus* (Figures 33, 35, 36).

Ponder (1968) interpreted *M. mariae* as a chronosubspecies of *M. espinosus* (Hutton, 1886), though Ben and Maxwell (1990) suggested that they might well be distinct species. Compared with 15 well preserved specimens of *M. espinosus* obtained near Waipukurau (GS10858, map ref. U22/085308, former cutting on disused section of Ashcott Road, WNW of Waipukurau, A.G. Ben, NZGS—lowest Nukumaruan, Late Pliocene), which are indistinguishable from the type material obtained nearby, *M. mariae* differs in having a protoconch that is shorter relative to its width with a shouldered (rarely rounded) instead of rounded, more or less bulbous first whorl (Figure 27), and in having narrower spiral interspaces, especially on the first three or four teleoconch whorls. In most specimens of *M. mariae* the secondary spiral cords enlarge to resemble the primaries more rapidly than in *M. espinosus*. Interestingly enough, the sample includes well-preserved specimens of a larger species that also lacks a shoulder angulation on the protoconch (Figure 30). The status of this larger fossil species is unclear, but it is certainly more closely related to *M. octogonus* than to *M. espinosus*. *Muricopsis espinosus* or a very similar species occurs in the bathyal “coral thicket”, Lake Ferry, Palliser Bay (Mangapanian: Late Pliocene) (Figure 31). The protoconch has thus independently become angulate in the *M. octogonus* and *M. mariae* lineages since the Pliocene. The differences between *M. espinosus* and *M. mariae* in protoconch morphology and similarities in teleoconch morphology suggest that they are distinct species.

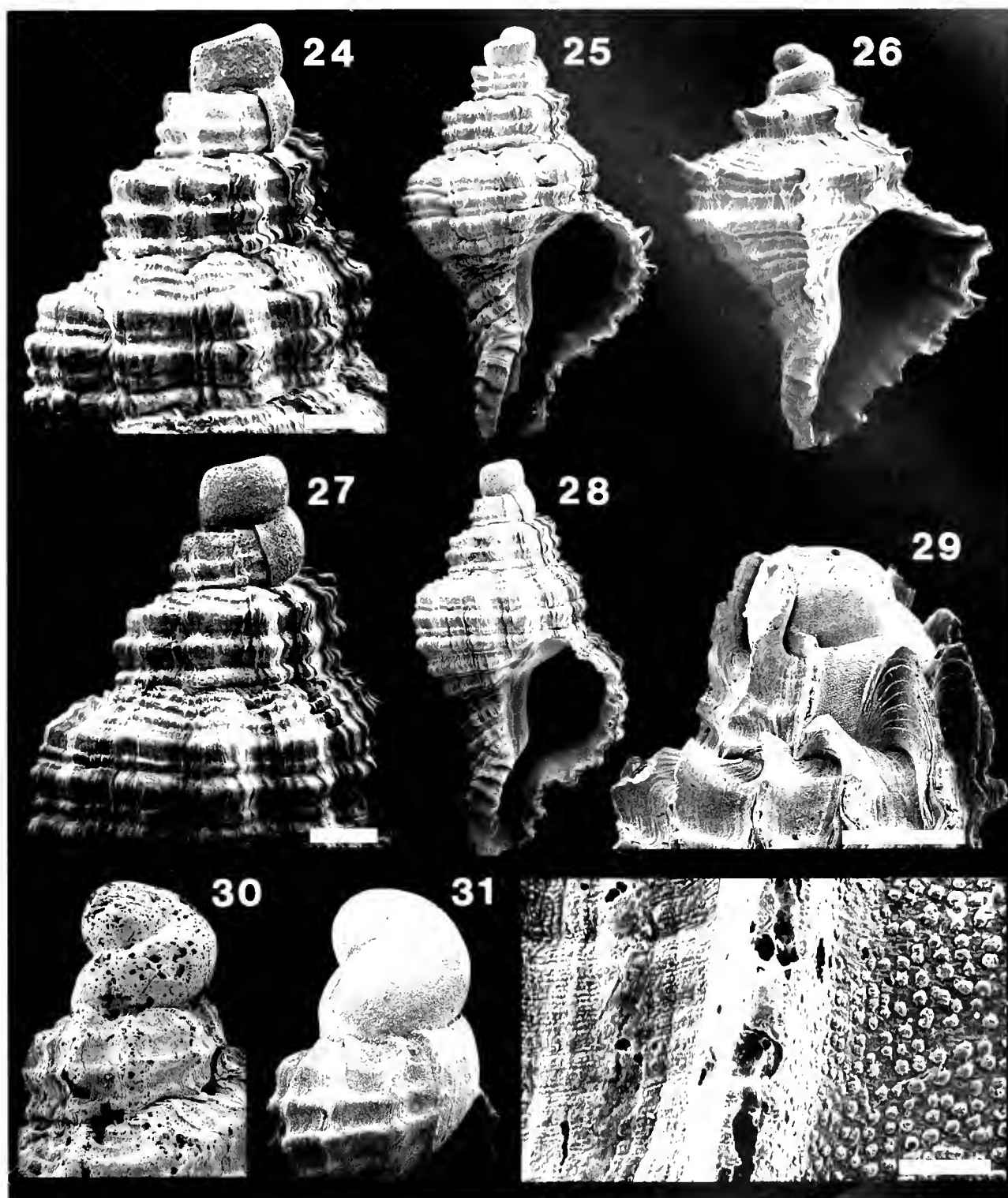
The original description of *Murex espinosus* (Hutton, 1886) is based on more than one specimen, the larger of which provided the cited dimensions (30.0×14.5 mm, CM3294), the smaller of which was subsequently illustrated by Hutton (1893) (28.0×13.3 mm, CM3295). Although these specimens each have two labels (none original) stating that they are “holotype” and “paratype” respectively, they are in fact syntypes because Hutton did not use these unequivocal terms. Ponder (1968, figs 35, 36) effectively designated the larger specimen as lectotype by stating that it was the “holotype”. Incidentally,

←

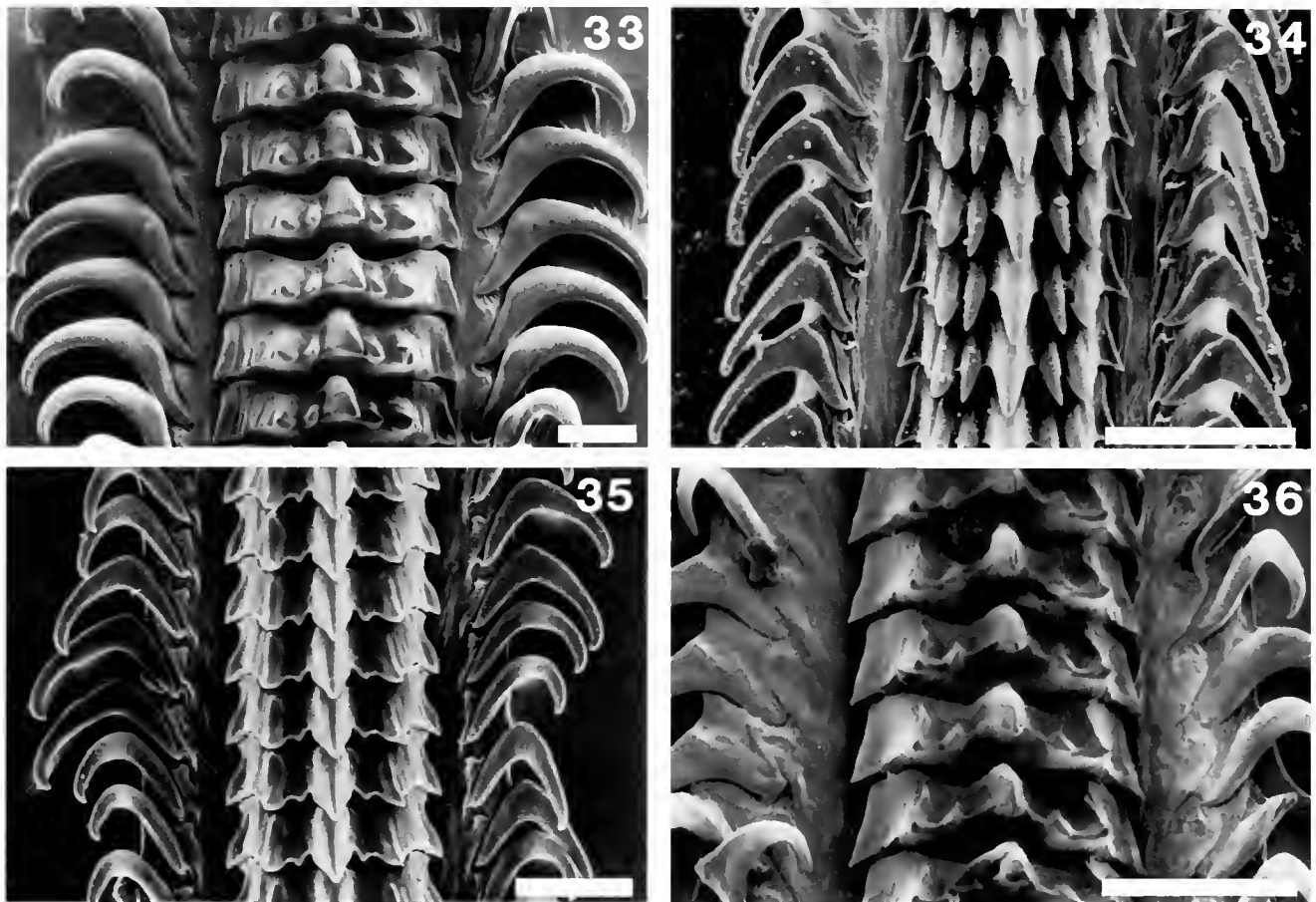
Figures 1–12. Shells of adult *Muricopsis* (*Murexsul*) *octogonus* (Quoy and Gaimard). 1. Off Thompson Point, Waiheke Island, 22 m, KWB (length 54 mm). 2. Off Cuvier Island, 70 m, M.5911 (length 78.5 mm). 3. Off Motukahan Island, W of Paparoa, Coramandel, 18–20 m, KWB (length 45.5 mm). 4. Scallop bed near Matiatia Bay entrance, Waiheke Island, 13 m, KWB (length 48 mm). 5. Off Three Kings Islands, craypot, KWB (length 90 mm, est. 93 mm). 6. Ranfurly Bank, East Cape, 31–47 m, M.75079 (length 46 mm). 7. Off Mayor Island, 59–74 m, M.64825 (length 63.5 mm). 8. Off Motuhoropapa Island, The Noises, 25 m, KWB (length 42.5 mm). 9. Off Spirits Bay, 48 m, M.137051 (length 54 mm). 10. Hooper Point, Spirits Bay, 12 m, M.134630 (length 29 mm). 11. Off Tom Bowling Bay, 49 m, M.137090 (length 64 mm). 12. Reotahi, Whangarei, low tide, KWB (length 45.5 mm).



Figures 13–23. Shells of *Muricopsis* species (all specimens adult except 18). 13–15, *Muricopsis* (*Murexsul*) *octogonus* (Quoy and Gaimard): 13, Rarifurly Bank, East Cape, 89–94 m, M.64812 (length 46 mm); 14, Whangaroa Harbour entrance, 25 m, M.74899 (length 38 mm); 15, originally figured syntype, MNHN (length 35.5 mm). 16, 23, *Murexsul* (*Muricopsis*) *profunda* new species, holotype, off Three Kings Islands, 91 m, M.70356. 17, 19, *Muricopsis* (*Murexsul*) *mariae* (Finlay): 17, Archway Island, Three Kings Islands, 15 m, M.117096 (22.3 × 12.3 mm); 19, Whangaroa Harbour entrance, 25 m, M.137244 (26 × 13 mm). 18, 20, *Murexsul* (*Rolandulla*) *undulatus* (Tenson Woods), Gull St Vincent, South Australia, South Australian Museum (Figure 20, length 32 mm). 21, 22, *Murexsul* (*Rolandulla*) *scotti* new species: 21, Holotype, Matheson's Bay, Leigh, 6–9 m, M.135186 (length 44 mm); 22, Paratype, Southeast Bay, Great Island, Three Kings Islands, 15 m, KWB (length 53.5 mm). Scale line = 1 mm.



Figures 24–32. Early whorls of *Muricopsis* species: **24, 25.** *Muricopsis* (*Murexsul*) *octogonus* (Quoy and Gaimard), Whangaroa Harbour entrance, 25 m, M 74899 (shell length 7.05 mm); **26.** *Murexsul* (*Rolandulla*) *scotti* new species, submarine cave S side of Rosemary Rock, Princes Islands, Three Kings Islands, 20 m, M 117084 (length 6 mm); **27, 28.** *Muricopsis* (*Murexsul*) *mariae* (Finlay), Whangaroa Harbour entrance, 25 m, M 137244 (shell length 4.75 mm); **29, 32.** *Muricopsis* (*Murexsul*) *profunda* new species, early whorls (29) and teleoconch (left) and protoconch (right) microsculpture (32), NW of Great Island, Three Kings Islands, 310 m, M 93876; **30.** *Muricopsis* (*Murexsul*) sp. aff. *octogonus* (Quoy and Gaimard), GS10855, Ashcott Road, Wapukuran, shallow water, Late Pliocene (lowest Nukunianian), NZGS TM8078; **31.** *Muricopsis* (*Murexsul*) sp. cf. *espinosus* (Hutton), 'coral thicket', Lake Ferry, Palliser Bay, bathyal, Late Pliocene (Mangapamian), M 10408. Scale line for figure 32 = 50 μ m; other scale lines = 500 μ m.



Figures 33–36. Radulae of *Muricopsis* species. **33.** *Muricopsis* (*Murexsul*) *octogonus* (Quoy and Gaimard), off Te Arai Point, Northland, 41 m, M.137251 (shell length 65 mm). **34.** *Muricopsis* (*Murexsul*) *mariae* (Finlay), Governors Pass, Great Barrier Island, 11–29 m, M.21784 (shell length 22 mm). **35.** *Muricopsis* (*Rolandiella*) *scotti* new species, off Cape Rodney, 11–13 m, M.137416 (shell length 40 mm). **36.** *Muricopsis* (*Rolandiella*) *umbilicatus* (Tenison Woods), Edithburgh, South Australia; South Australian Museum, Adelaide, unregistered (shell length 28 mm). Scale lines = 50 μ m.

this type material was mislaid until recently, and omitted from the catalogue of type and figured fossils in the Geology Department of the Canterbury Museum (Bradshaw *et al.*, 1992).

Muricopsis (*Murexsul*) *profunda* new species
(Figures 16, 23, 29, 39)

Description: Shell up to 10.5 mm high (holotype adult?), fusiform, of moderate thickness; protoconch and teleoconch pale orange, adapical 4 primary spirals and secondary spirals between them reddish brown on last whorl. Protoconch 830–870 μ m wide excluding flared rim, of 1.5 convex whorls, covered with minute hemispherical granules, summit of first whorl angulate, last half whorl rather evenly convex. Teleoconch of 4.5 regularly expanding whorls; first whorl broadly convex; subsequent whorls with pronounced supramedian angulation, sutural ramp broad and flat, side broadly convex, smoothly confluent with siphonal canal. Sculpture consisting of axial varices, and rounded primary and sec-

ondary spiral cords. Axial varices strongly retracted from adapical insertion throughout, 12 on last whorl (holotype), narrow on 1st whorl, sloping adaxially so that bases are overhung, blade like and strongly adapically produced above protoconch/teleoconch suture and cemented to side of last whorl of protoconch, extending beyond adapical extremity of last protoconch whorl or to about mid whorl length. Axial varices on subsequent whorls becoming thicker and rounded, each surmounted by 4 or 5 fine, collabral, adaxially sloping, axial lamellae. Axial interspaces with fine collabral growth lines and a few lamellar growth lines. Primary spiral cords numbering 3 on spire and 3 on base; spire spirals commencing immediately, similar throughout, adapical spiral at shoulder angulation, abapical spiral bordering suture; adapical 2 basal spirals similar to spire spirals, abapical spiral stronger, widely separated. Secondary spirals numbering commencing on 3rd whorl, remaining weaker than primaries, 2 on ramp, 1 between each primary spiral, 3 between abapical basal primaries, and 1 between abapical basal primary and tip of canal. Siphonal canal of moderate



Figures 37. Distributions of New Zealand Recent *Muricopsis* (*Murexsul*) *octogonus* (Quoy and Gaimard) (500 and 1000 m isobaths indicated).

length, gently flexed, partly enclosed by thin extension of inner lip. Aperture pyriform; outer lip rather thin at rim, weakly thickened within, simple; inner lip fully adherent adapically, rim free at abapical extremity and extending almost to canal tip. Animal unknown.

Type material: Holotype NMNZ M.70356, 34°11'S, 172°10'E, off Three Kings Islands, northern New Zealand, 91 m, 19 February 1974, r.v. *Achcron*. Paratypes: 33°59.2'S, 172°13.6'E, 18 km N of Great Island, Three Kings Islands, 155 m, 23 June 1978, r.v. *Tangaroa* (1 juvenile, M.137247); 34°06.5'S, 172°04.7'E, 11 km NW of Great Island, 310 m, 30 June 1978, r.v. *Tangaroa* (1 juvenile, M.93876).

Other material examined: 34°00.9'S, 171°44.7'E, Middlesex Bank, NW of Three Kings Islands, 201–216 m, 31 January 1981, r.v. *Tangaroa* (2 juveniles, M.93302); 34°02.0'S, 171°44.0'E, Middlesex Bank, 246–291 m, 31 January 1981, r.v. *Tangaroa* (3 juveniles, M.137245); 34°05.9'S, 171°55.1'E, 24 km NW of Great Island, Three Kings Islands, 710 m, 27 June 1978, r.v. *Tangaroa* (4 juveniles, M.137246); 34°17.6'S, 171°45.3'E, 39 km SW of Great Island, 427 m, 21 June 1978, r.v. *Tangaroa* (3 juveniles, M.94338).

Distribution: Off Three Kings Islands, northern New Zealand, 91–710 m (shells only).

Remarks: *Muricopsis profunda* differs from *M. octogonus* and *M. mariae* principally in having axial varices that ride up onto the protoconch from the next whorl, in that the outer lip is much more strongly retracted



Figure 38. Distributions of New Zealand Recent *Muricopsis* (*Murexsul*) *mariae* (Finlay) (500 and 1000 m isobaths indicated).

from the suture, and in that the spiral cords are stronger at equivalent stages of growth and become pigmented at a later stage of growth. The size attained by this species is unclear, though it may not grow much larger than the holotype (length 10.5 mm).

Etymology: Deep (Latin).

Rolandiella new subgenus (of *Muricopsis*)

Type species: *Muricopsis* (*Rolandiella*) *scotti* new species; Recent, northern New Zealand.

Diagnosis: Shell similar to those of species of *Muricopsis* (*Murexsul*), but with median shoulder angulation and weak abapical 2 primary spiral cords on first 1.5 teleoconch whorls. Inner lip of most specimens upstanding over most of its length.

Description: Shell 21–62 mm high at maturity, spire about as high as last adult whorl or slightly shorter, stout, of moderate thickness. Protoconch of 1.5–2.0 rounded whorls. Teleoconch of mature specimens with 5.5–7.0 convex, shouldered whorls, shoulder median on first 2 whorls, ascending to adapical third or slightly higher on subsequent whorls; sutural ramp shallowly concave; side broadly convex, smoothly confluent with siphonal canal. Primary sculpture consisting of strong, axial varices and spiral cords with spines at intersections. Varices traversing all whorls, angulate in section, numbering 8–11 (7 or 12 in occasional specimens) on adult penultimate whorl. Primary spiral cords rounded, numbering 3 on spire and 3 on base in adults. Adapical primary spiral at

shoulder angulation, peripheral; abapical primary bordering suture throughout, or separating as insertion of last few whorls descends to next primary spiral; adapical and abapical primaries commencing immediately; intermediate primary commencing at about mid first whorl, gradually enlarging to resemble other primaries. Abapical basal primary spiral widely separated from adjacent primary, interspaces of other primary spirals closer and of similar width to each other. Secondary spirals progressively developing, 1–5 on sutural ramp, 1 each in some or all interspaces of primary spirals, 0–3 between abapical basal primary spiral and tip of canal, others on summits of some or all primary spirals, 1 or more enlarging to resemble primaries on last adult whorl. Primary and 1 (abapical shoulder spiral) or more secondary spirals produced as short to moderate-length spines at varices, spines on primary spirals of similar length or shoulder spiral longest. Secondary axial sculpture comprising fine collabral growth lines that are raised as thin, fragile lamellae on ramp against suture and where intersecting spiral sculpture. Aperture pyriform. Outer lip thickened within at maturity, strongly so in particularly large specimens, which may also develop spirally elongate denticles. Inner lip thin, fully adherent over adapical third or quarter, abapical part typically free, flared and strongly projecting, abapical extremity extending well beyond flexure of siphonal canal. Siphonal canal of moderate length, almost enclosed by infolding; siphonal fasciole strong, forming an umbilicus in some very large specimens. Radula and operculum similar to those in *Muricopsis* (s. str.) and *Murexsul*.

Remarks: *Rolandiella* is introduced for *Muricopsis* *scotti* new species from northern New Zealand, and *M. umbilicatus* (Tenison Woods, 1876) from southern Australia, both of which resemble typical *Murexsul* species in gross facies, but differ in that the shoulder spiral is situated medially on the early spire whorls then ascends adapically, and the intermediate primary spiral on the spire commences later than the others and develops slowly. By contrast, in *Muricopsis* species, all three primaries are strong and commence immediately on the first teleoconch whorl, and the shoulder spiral borders the suture then descends abapically over subsequent whorls.

None of the named New Zealand Cenozoic species referred to *Murexsul* by Beu and Maxwell (1990) seem to belong in *Muricopsis* (*Rolandiella*), though the relationships of the Early Miocene species *Muricopsis echinophorus* (Powell and Bartrum, 1929) are unclear because the early teleoconch morphology is unknown.

Both *M. (Rolandiella) scotti* and *M. (R.) umbilicatus* have large, rounded, paucispiral protoconchs indicating non-planktotrophic development, and suggesting that they have either crawl-away larvae or drifting larval stages of short duration. We suppose that they are derived from a common ancestor with planktotrophic larval development that had a trans-Tasman distribution. How far back in time this putative common ancestor may have

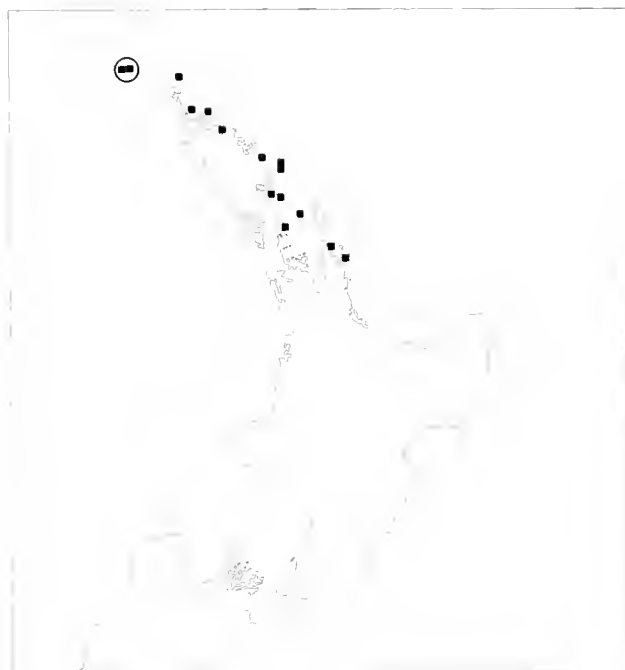


Figure 39. Distributions of New Zealand Recent *Muricopsis* (*Murexsul*) *profunda* new species (circle) and *Muricopsis* (*Rolandiella*) *scotti* new species (squares) (500 and 1000 m isobaths indicated).

lived is impossible to estimate without fossil records or molecular data.

Etymology: After Roland Houart, Belgium, in appreciation of his outstanding contribution to world muricid systematics.

Muricopsis (Rolandiella) scotti new species
(Figures 21, 22, 26, 35, 39)

Muricopsis species Scott, 1989: 6, text figs.

Muricopsis octogonus.—Hart, 1993: 45, right text fig. only (=holotype). Not Quoy and Gaimard, 1833.

Description: Shell up to 62 mm high, fusiform, spire about as high as last adult whorl or slightly shorter, stout, of moderate thickness. Protoconch and first 1 or 2 teleoconch whorls white, subsequent whorls white or pale buff, primary, secondary and some finer spiral cords reddish brown, aperture porcellaneous white. Protoconch sharply delineated by low varix, of 1.5–2.0 smooth, convex whorls. Teleoconch of up to 7 convex, shouldered whorls, shoulder median on first 2 whorls, ascending to adapical third or slightly higher on subsequent whorls; sutural ramp shallowly concave; side broadly convex, smoothly confluent with siphonal canal. Primary sculpture consisting of strong, axial varices and spiral cords with spines at intersections. Varices traversing all whorls, angulate in section, numbering 8–11 (7 or 12 in occasional specimens) on adult penultimate whorl. Primary spiral cords rounded, numbering 3 on spire and 3 on base in adults. Adapical primary spiral at shoulder an-

gulation, peripheral; abapical spire spiral bordering suture at first, separating as insertion of last few whorls descends to next (formerly adapical basal) primary spiral; adapical and abapical spire spirals commencing immediately; intermediate spire spiral commencing at about mid first whorl, slowly enlarging to resemble abapical spire spiral and basal primary spirals. Abapical basal primary spiral widely separated from adjacent primary; interspaces of other primary spirals closer and of similar width to each other. Secondary spirals appearing progressively, numbering 3–5 on sutural ramp, 5–7 in zone comprising summit of shoulder spiral space between it and adjacent primary; usually 3 or 4 on summits of other primary spire spirals, 3 or 4 between abapical 2 basal primaries, 3 between abapical basal primary spiral and tip of canal, and generally 1 each in some or all interspaces of primary spirals, most or all secondaries remaining weaker than primaries throughout, or some enlarging to resemble primaries on last adult whorl. Primary and some secondary spirals produced as short to moderate-length spines at varices, shoulder spines longer than others on spire, spines on larger spirals typically of similar length on last adult whorl. Secondary axial sculpture comprising fine collabral growth lines that are raised as thin, fragile lamellae on ramp against suture and where intersecting spiral sculpture. Aperture pyriform. Outer lip thickened within at maturity, strongly so in particularly large specimens, which may also develop spirally elongate denticles. Inner lip thin, fully adherent over adapical third or quarter, abapical part typically free, flared and strongly projecting, abapical extremity extending well beyond flexure of siphonal canal. Siphonal canal of moderate length, almost enclosed by infolding; siphonal fasciole strong, forming an umbilicus in some very large specimens. Operculum with terminal nucleus, yellowish brown. Radula (figure 35): Central teeth each with strong, conical central cusp; smaller, conical lateral and marginal cusps, and 2 very small inner lateral denticles that are well separated from lateral cusp. Lateral teeth narrow.

Type material: Holotype NMNZ M.138186, Mathesons Bay, Leigh, northern New Zealand, 6–9 m, February–March 1992, D.W. Gibbs (ex D.W. Gibbs and K.W. Burch collections). Paratypes: 34°09.5'S, 172°08.8'E, Southeast Bay, Great Island, Three Kings Islands, 20–22 m, 4 March 1997, K.W. Burch and D.D. Crosby (2 juveniles, M.134760); Southeast Bay, alive, 18 m, 18 May 1982, K.W. Burch (6, KWB); Princes Islands, Three Kings Islands, 15 m, 29 November 1983, G.S. Hardy and A.L. Stewart (1, M.75135); S side of Southwest Island, Three Kings Islands, alive, 27 m, 12 February 1986, G.S. Hardy (2, M.84267); off Cape Maria van Diemen, craypot, May 1991 (1, KWB); Whangaroa Harbour entrance, alive, 18 m, November 1995, K.W. Burch and D.W. Gibbs (2, KWB); Rikoriko Cave, Poor Knights Islands, alive, 30–40 m, 1982, M.H.B. O'Neill (1, M.75181); Poor Knights Islands, alive, May 1979, A.S.W. Penniket (1, M.133691); Poor Knights Islands,

December 1980, K.W. Burch (1, M.133692); Poor Knights Islands, alive, 15–20 m, 1983, K.W. Burch (4, KWB); Poor Knights Islands, alive, 1970, 1972, W. Doak (5, M.133690); South Cave, Poor Knights Islands, alive, 17 m, 21 May 1969, A.N. Baker (1, M.23617); South Harbour, Poor Knights Islands, alive, 25 May 1969, A.N. Baker (3, M.23618); off Cape Karikari, 30 m, 20 June 1981 (1, M.133694); Urquarts Bay, Whangarei Heads, alive, March 1965 (1, M.133695); "The Canyon", N side of Burgess Island, Mokohinau Islands, alive, 15–21 m, January 1985, D.W. Gibbs (3, KWB); Maori Island, Leigh, 22 May 1975, A.S.W. Penniket (1, M.133695); NE of Mathesons Bay, Leigh, alive, 18 m, May 1995, D.W. Gibbs (1, M.127040); Mathesons Bay, alive, 6–10 m, February–March 1992, D.W. Gibbs (6, KWB); S of entrance to Omaha Cove, Leigh, 20 m, December 1967, I. Scott (2, IS); off Little Barrier Island, alive, craypot, T. Riley (2, M.133693); Cape Rodney, alive, 15 m, June 1987, D.W. Gibbs (7, M.90125); Cape Rodney, alive, 15 m, 4 March 1989, I. Scott (12, M.117277); Cape Rodney, alive, 11–13 m, I. Scott, May 1989 (53, M.137416); Cape Rodney, alive, 18 m, June 1977 (1, M.133698); Waikawau Bay, Coromandel, alive, 16 m, April 1989, D.W. Gibbs (2, KWB); off Needle Island, Mercury Bay, alive, 16 m, January 1985, D.W. Gibbs (3, KWB).

Other material examined: S side of Rosemary Rock, Princes Islands, Three Kings Islands, 20 m, 18 January 1985, F.J. Brook (5, M.117084); off West Island, Three Kings Islands, *Elingamite* wreck, alive, W. Doak (1, M.133696); 34°20.0'S, 173°06.6'E, N of North Cape, 163–168 m, 27 January 1981, r.v. *Tangaroa* (1, M.137225); Rarawa Reef, Great Exhibition Bay, craypots, alive, 40 m, August 1989, I. McMillan (2, M.100382); Rarawa Reef, craypots, alive, 73 m, 28 September 1988, I. McMillan (6, M.95234); Rarawa Reef, craypots, alive, 40 m, 16 December 1987, I. McMillan (3, M.95315); off Cape Karikari, alive, craypots, 1988, I. McMillan (1, M.95322); Henry Island, Whangaruru, alive, 13 m, 5 December 1971, A.N. Baker (1, M.25920); off Hen and Chickens Islands, alive (1, M.2686; 1, M.83882); Mathesons Bay, Leigh, alive, 15–20 m, 26 March 1995, A. Spurgeon (2, M.126998).

Distribution (Figure 39): Three Kings Islands and northeastern North Island, New Zealand as far south as Little Barrier Island, 13–168 m; taken alive at 13–40 m from rocky ground.

Remarks: *Muricopsis scotti* is most similar to the southern Australian species *M. umbilicatus* (Figures 18, 20, 26) in early shell ontogeny and gross adult shell facies than to any New Zealand Recent *Murexsul* species. *Muricopsis scotti* differs from *M. umbilicatus* in a number of details including larger adult size (shell length 34–62 mm versus 21–30 mm), stronger and more numerous secondary spirals, insertion point of the last few whorls descending from the abapical spire spiral to the next (formerly adapical basal) primary spiral, and abapical secondary spiral on the sutural ramp never becoming as

large as the shoulder spiral. The radula of *M. scotti* is similar to those of *M. umbilicatus* and *M. octogonus* (Figures 3, 35, 36).

Muricopsis scotti resembles *M. octogonus* in size, but is readily distinguishable by the following characteristics: orange brown instead of dark reddish brown operculum, rounded instead of angulate protoconch, generally larger aperture, shorter siphonal canal, and much stronger secondary spiral sculpture on the primary spiral cords, especially on the shoulder spiral and between it and the adjacent primary. Unlike *M. octogonus*, which has extremely variable sculpture, *M. scotti* consistently has a distinct shoulder angulation, angular varices and short spines that are not curved backwards, or at most only slightly so. In *M. scotti* the shoulder spiral (adapical primary) is much stronger than the others on the first two teleoconch whorls and occupies a median position, then gradually ascends to about the adapical third on subsequent whorls (Figure 26). By contrast, on the first 1.5 teleoconch whorls in *M. octogonus*, the three primary spire spirals are all strong and similar, and the shoulder spiral commences beside the suture and descends to about the adapical third, remaining there or at the adapical quarter on subsequent whorls (Figure 24). Although the rim of the inner lip may be upstanding or more or less fully adherent in both species, that in *M. scotti* is typically free and more strongly upstanding abapically, and extends abapically further beyond the angulation at the top of the siphonal canal.

Shells of living *M. scotti* are invariably more or less covered with living Bryozoa, barnacles and other epibionts, often with the addition of *Waltonia inconspicua* (Sowerby, 1846) (Brachiopoda), upon which it has been observed to feed (Scott, 1989 and pers. comm; K.W.B., pers. obs.).

Etymology: After Ian Scott, Auckland.

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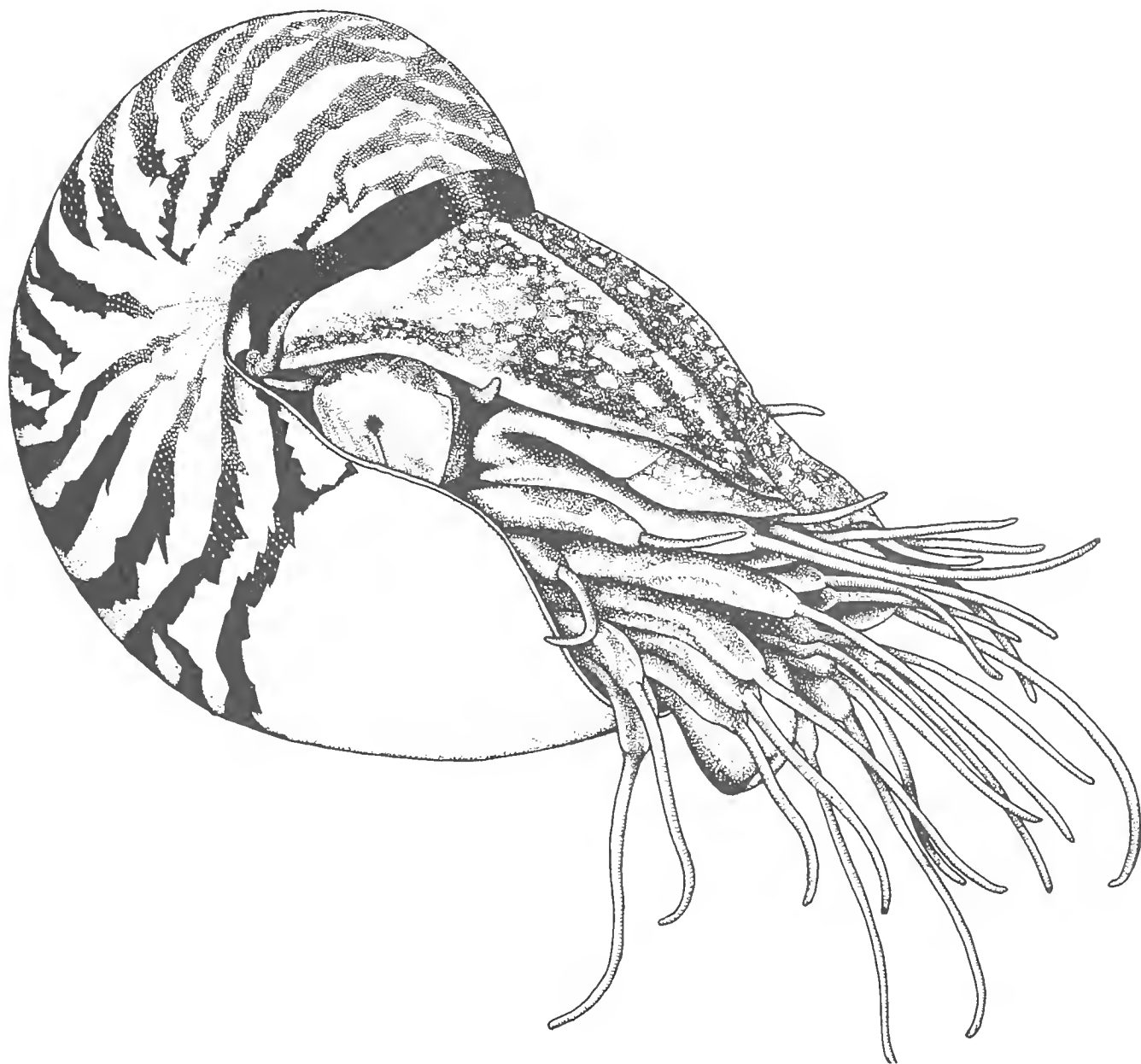
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Notes on the taxonomy of introduced *Bellamyia* (Gastropoda: Viviparidae) species in northeastern North America

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ABSTRACT

The genus *Bellamyia* has become well established in North America since its first introduction around the turn of the 20th century. Some malacologists have recognized two species, usually placed in the genus *Cipangopaludina*, *C. chinensis*, and *C. japonica*. Other investigators, however, have questioned a two species concept or simply considered all populations to be variants of a single species, *C. chinensis*. Differences observed in the juvenile shell and male reproductive anatomy, along with size-specific features of adult shells, enable easy separation of the two taxa and support the two species concept. Characters of female and male reproductive anatomy confirms the placement of the species in the subfamily Bellamyinae. Anatomical features which have been used to substantiate *Cipangopaludina* are proposed to be of subgeneric value only.

Key words: Introduced snails, *Cipangopaludina*, *Idiopoma*, *Viviparus*, *Lecythoconcha*.

INTRODUCTION

Among the more conspicuous members of the North American freshwater gastropod fauna are the large exotic viviparid snails customarily placed in the genus *Cipangopaludina*. The North American history of *Cipangopaludina* and its distribution was discussed and reviewed by Clench and Fuller (1965) (as a subgenus of *Viviparus*), Dundee (1974), and Jokinen (1982). The majority of North American populations are confined to the coasts, with scattered records from the interior. At present, the east coast appears to comprise the greatest number of occurrences (Jokinen, 1982).

Since the earliest reports of *Cipangopaludina* populations in North America around 1900 there has been much debate regarding the identification and validity of the various species and subspecies reported and, to a lesser extent, the status and position of the taxon *Cipangopaludina* in the Viviparidae. Hannibal (1912) proposed the subgenus *Cipangopaludina* to accommodate *Idiopoma malleata* (Reeve, 1863), leaving *I. japonica* (von Martens, 1861) in *Idiopoma* s. s. Subsequent authors (e.g.,

Annandale, 1920; Prashad, 1928) regarded *Idiopoma* Pilsbry, 1901, recognized primarily on features of the operculum, as a synonym of *Viviparus*. Annandale (1920) used anatomical characters to propose a new genus *Lecythoconcha* to include *L. chinensis* and, in a later paper (Annandale, 1921), to include *L. japonica* as well. Rao (1925) maintained use of *Lecythoconcha* and expanded the number of anatomical characters that define the genus, most notably a folded and thickened gill filament, a thickened muscular mantle edge, and the "strongly developed brain". Prashad (1928) subsequently synonymized *Lecythoconcha* with *Cipangopaludina* but retained *Lecythoconcha* as a subgenus. Furthermore, he reduced *Idiopoma malleata* to a subspecies of *V. chinensis* (Gray, 1817). Kuroda (1929) adopted all of Prashad's (1928) revisions. Rohrbach (1937) primarily used characters of the reproductive anatomy to divide the viviparids into two subfamilies, the Viviparinae and a new subfamily Bellamyinae. Under the Bellamyinae he listed a single large genus, *Bellamyia* Jousseaume. Although considered to be a genus largely limited to tropical species, Rohrbach (1937) was able to examine specimens of a race of non-tropical *V. chinensis* that displayed anatomical features of *Bellamyia*. Yen (1943) extended Rohrbach's (1937) classification to Chinese species and subspecies, restated the close relationship between *Bellamyia* and *Cipangopaludina*, but retained *Cipangopaludina* at the genus level.

The first major work on North American viviparids following this period is Clench and Fuller's (1965) study in which, for unknown reasons, they treat *Cipangopaludina* as a subgenus of *Viviparus*. These authors resurrected the trinomen *V. chinensis malleatus* for all North American populations of this species and listed it as a species separated from *V. (Cipangopaludina) japonicus*. Most subsequent studies on viviparid faunas (e.g. Pace, 1973; Taylor, 1981; Rao, 1989) have considered *Cipangopaludina* a genus of the Bellamyinae.

North American opinion has been divided concerning the validity of the two introduced species (see Jokinen,

1991, for review). Many North American faunal studies including these viviparids have listed all large introduced viviparid populations with unbanded shells as *Cipangopaludina chinensis* (eg. Robertson and Blakeslee, 1948; Jacobson and Emerson, 1961; Dundee, 1974; Clarke, 1978). Other reports have recognized the two species *C. chinensis* and *C. japonica* (eg. Wolfert and Hiltunen, 1968; Burch, 1982; Taylor, 1981; Jokinen, 1983, 1991; Smith, 1995).

Certainly one of the problems affecting the species issue is the apparent rarity of the taxon *C. japonica*. Clench and Fuller (1965) gave only four North American records, and Taylor (1981) listed only one in California. Wolfert and Hiltunen (1968) listed an Ohio record and Jokinen (1984) provided an additional record in Connecticut, but has before and since considered the population *C. chinensis* or doubtfully *C. japonica* (Jokinen, 1983, pers. comm.). Jokinen (1991) subsequently added a New York record that would be the eighth published North American record for *C. japonica*.

The impetus for the present study came from the discovery of two wild, previously unreported populations of *C. japonica*-morph snails in Connecticut from which several variously aged specimens and reproductively active females were collected. The present study provides comparative data on a number of characters of each species in an attempt to determine whether two species or a single variable species occurs in North America. Additionally, using data from reproductive organs and other anatomical characters plus observations by previous authors on viviparid subgroups, a proposal to reduce *Cipangopaludina* to a subgenus of *Bellamya* is presented. Hereafter in this study these two species will be referred to as *Bellamya* spp.

MATERIALS AND METHODS

Specimens from 12 extant or extirpated *Bellamya* populations were examined. The original assignment of specimens to either specific taxon was by use of adult shell characters. The distribution of specimens is listed below. All were fixed in 10% formalin, relaxed or unrelaxed, and stored intact in 50–60% isopropyl alcohol. Intact shells of deceased animals were also collected. Each collection has been catalogued in the Invertebrate Division, Museum of Zoology, University of Massachusetts, Amherst (UMA). Collection numbers and other details regarding the collections can be furnished upon request.

Bellamya chinensis s.l.: UMA 0668, University Pond, University of Massachusetts Campus, Amherst, Hampshire County; UMA 0885, unnamed pond in Medford, and UMA 1705, Lake Winthrop, Holliston, both Middlesex County; UMA 1635, Forest Park Ponds, Springfield, Hampden County; UMA 1663, Wachusett Reservoir Outlet, Worcester County; UMA 1094, Purchase Louisiana Brook, Northfield, Franklin County; UMA 1330, Pine Tree Brook, Milton, Norfolk County; UMA 1805, Snake River, Norton, Bristol County (all Massa-

chusetts); UMA 1755, Black Pond, Middlefield, Middlesex County, Connecticut.

Bellamya japonica: UMA 1754, Lake Mohegan, Fairfield, Fairfield County; UMA 1816, Connecticut River, Lyme, New London County; UMA 1755a, Black Pond, Middlefield, Middlesex County, all Connecticut. Also examined were specimens (UMA 1700) purchased from a pet store in Hadley, Hampshire County, Massachusetts.

Samples of intra-uterine juveniles were removed from females. The animal was removed from the shell of each juvenile and the shell air dried. Radulae were also removed from adult specimens, cleaned in 10% potassium hydroxide, subsequently washed, and air dried. All dried material was mounted on individual Cambridge stubs with Duco cement and sputter-coated with gold. All prepared specimens were then examined with a JEOL Model JSM-5200 scanning electron microscope (SEM).

For anatomical study, at least five specimens of each sex were dissected from the two largest collections of each species as determined by shell characters. Thereafter, dissections were made on at least one adult specimen of each sex (if available) from each remaining location. A total of 44 specimens divided almost evenly among both species were analyzed. Dissections were performed with the aid of a Wild M5 dissecting microscope.

RESULTS

The principal conchological characters distinguishing the two taxa are the shape of the spire and the presence of carination; to quote from Clench and Fuller (1965) regarding *B. japonica*: "...can be distinguished from *V. malleatus* (= *C. chinensis*) by having a more acute spire and by having fine carina or carinae." An examination of animals from presumed *B. japonica* populations reveal that these characteristics are most evident in shells 35–45 mm shell length (Figure 1). At this size, the species can be separated using the diagnosis of Clench and Fuller (1965). Below 35 mm shell length both species have a carina on the body whorl. Above 45 mm, the carina of *B. japonica* becomes nearly obsolete, and only a slightly more acute spire in *B. japonica* enables identification.

The source of differentiation in shell characters in these two species is in part derived from an allometric growth pattern first described by Jokinen (1982), who showed that shell width in *B. japonica* increases at a slower rate than in *B. chinensis*. This phenomenon would account for the more "acute spire" in *B. japonica* described by Clench and Fuller (1965). The regression slopes for each species, however, are only slightly different (see Jokinen, 1982, fig. 2). Therefore, adult shell morphology has its limitations in the distinction of these two species.

A characteristic that appears to be reliable in separating *B. japonica* from *B. chinensis* is the morphology of the intra-uterine juvenile shell. The juveniles occurring in the uterus or brood chamber, considered a functional

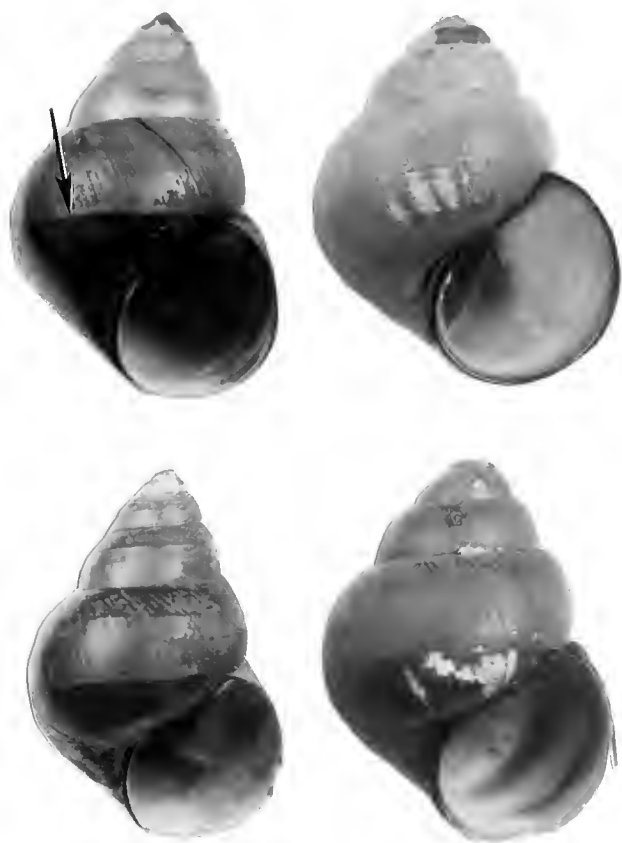


Figure 1. Comparison of similar sized shells of *Bellamya*. Upper and lower left, *B. japonica* from Lake Mohegan, Connecticut. Upper right, *B. chinensis* from Medford, Massachusetts, and lower right, *B. chinensis* from Black Pond, Connecticut. Arrow denotes carina. Scale line = 10 mm.

modification of what is otherwise called the pallial oviduct, demonstrate clear differences in the position of the embryonic whorl (protoconch) and in surface sculpture. Most viviparid snails in their juvenile stages have specific features of the periostracum, including the presence of periostracal hairs encircling the shell whorls, and surface sculpture (Fretter and Graham, 1962; Jokinen, 1984).

In the juvenile shell of *B. chinensis*, the spire comprises only two elevated whorls (Figures 2–4). The embryonic whorl is depressed in frontal view below the successive whorl (first teloconch whorl), characterized by two lines of periostracal hairs, one clearly evident on the whorl, the other along the upper border (Figure 2, arrow). Such was observed in all examined populations. In contrast, the embryonic whorl of *B. japonica* (Figure 5) is somewhat elevated above the first teloconch whorl, indicated by two spiral lines of periostracal hairs, which in frontal view gives the shell the appearance of having four whorls.

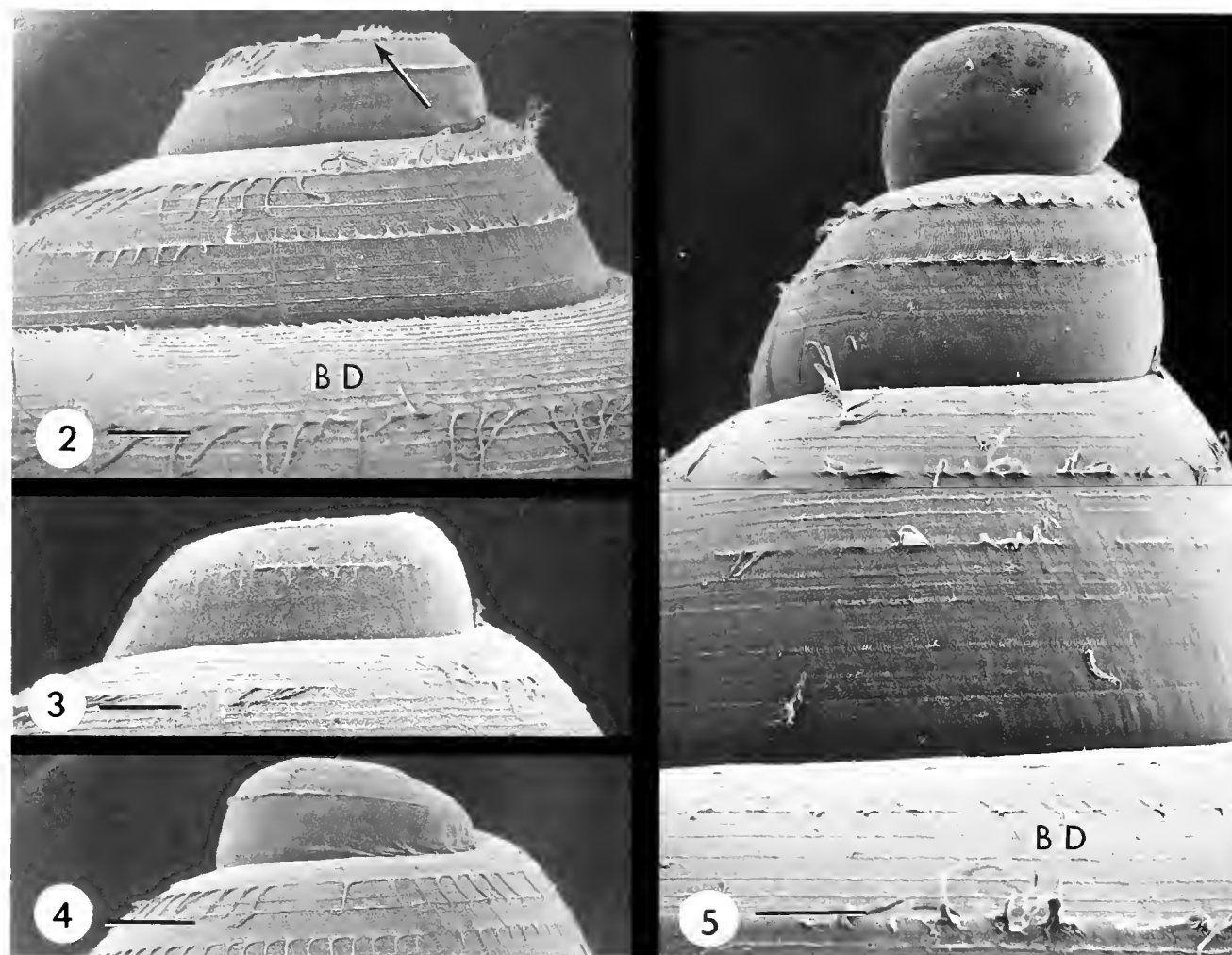
Differences in periostracum are even more evident than those in whorl development. The periostracum of the body whorl of juvenile *B. chinensis* (Figures 6, 7) is

finely sculptured with a series of closely set striae, about 20/mm near the midpoint of the body whorl, interrupted by perpendicular shallow grooves more widely spaced than the striae. The spiral lines bearing the fine hairs are not raised as spiral carinae. In *B. japonica* (Figure 8), the surface of the periostracum is strongly marked by raised carinae, each having a series of periostracal hairs. Between the carinae are widely spaced spiral striae, about 8/mm near the middle of the whorl. Although occasional interruptions occur, there is no pattern of distinct grooves as found in and characteristic of *B. chinensis*.

Regarding anatomical characters, the radula provides no specific or distinctive characters for interspecific differentiation. Very subtle differences (Figures 9, 10) occur in the spacing of denticles of the lateral teeth for example, but these differences are probably subject to variation and should not be considered as reliable taxonomic characters. The gill filament of each species consists of an elongate structure, measuring up to 5 mm length in the largest (>50 mm shell length) individuals. The filament is broadest at its base where it is attached to the mantle, narrowing in depth distally. A distinct blood vessel courses its length just below the thickened superior margin. The “folding” of the filament described by Rao (1925) in a few species, and used subsequently as a character of *Cipangopaludina*, was not observed in material of either species.

Major features of both the male and female reproductive systems demonstrate an overall conservative structural plan clearly characteristic of the Bellamyinae as defined by Rohrbach (1937). Dissection of the female reproductive system revealed no consistent differences between *B. chinensis* and *B. japonica*. Within the male reproductive system, the vas deferens of each species shows distinct differences in its dimensions and its relationship with both the columellar muscle and the testes. In *B. chinensis* (Figure 11), the vas deferens arises from the testes as an unbranched tube. All further branching of the vas deferens occurs internally within the testes. Occasionally, a single large anterior branch merging with the vas deferens is partially visible. The emerged vas deferens widens considerably as a complex duct and proceeds a short distance, suspended by mesenteries, until it reaches the columellar muscle. At this point, the remaining portion of the vas deferens bends sharply downwards. It then abruptly and without enlargement enters the prostate. The downwardly directed portion of the vas deferens remains free of the columellar muscle although it is supported throughout by mesentery tissue.

The vas deferens of *B. japonica* departs from the testes multibranched, with at least three and usually four visible branches converging to a single duct (Figure 12). The duct then enlarges, but not to the degree seen in *B. chinensis*, and extends a greater distance, suspended by mesentery tissue, until meeting with the columellar muscle where, as in *B. chinensis*, it bends downward and, without enlargement, joins the prostate gland. Un-



Figures 2–5. Spire of juvenile shells of *Bellamyia*. **2–4.** *Bellamyia chinensis*. **2.** Black Pond, Connecticut. **3.** Wachusett Reservoir, Massachusetts. **4.** Campus pond, Amherst, Massachusetts. Figures 3, 4, apical whorls only. **5.** *Bellamyia japonica*, Lake Mohegan, Connecticut. BD = body whorl. Scale line = 0.5 mm.

like *B. chinensis*, however, the portion of the vas deferens proximal to the prostate gland is invested with columellar muscle tissue. Other aspects of gross anatomy of the male reproductive system, including testes size and shape and prostate size and shape, are similar in the two species.

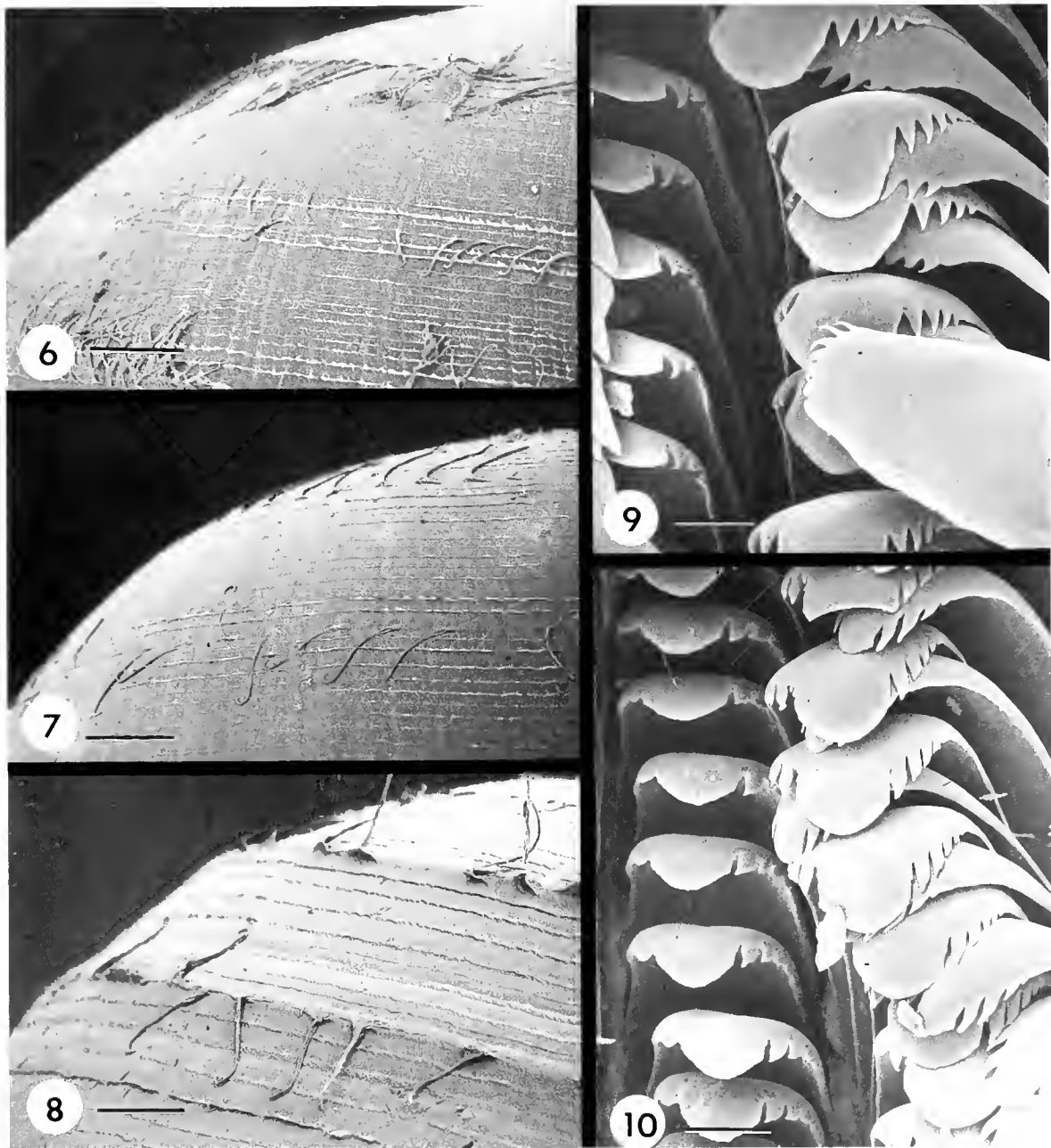
The characteristics of the vas deferens in each species were most pronounced in the larger animals. The two patterns were concordant with shell characters in all but one case, the Black Pond locality. Both species occur in this pond and examined males show features of shell and reproductive anatomy consistent with above observations or variations of each. Most males from this collection, however, are young adults (<35 mm shell length) and, as stated above, the anatomical characters indicative of each species are best developed in larger specimens. Nevertheless, it is possible that hybridization is occurring. Previously, in North America, both species have been reported in sympatry (Lake Erie; Wolfert and Hil-

tunen, 1968), but not in syntopy so it is not known if hybridization is a usual outcome of contact.

DISCUSSION

Although adult shell structure as presented by Clench and Fuller (1965) does not in and of itself provide convincing evidence for the recognition of two distinct species, the characters of the embryonic shell and male reproductive system in combination with shell features indicate that at least two similar but distinct species of *Bellamyia* are present in North America. The question remains, however, regarding which names to assign these species; is enough information available to warrant use of the two specific epithets, *malleata* and *japonica* as listed by Hannibal (1911) soon after the species were first reported in North America? If so, then what is the status of the name *B. chinensis*?

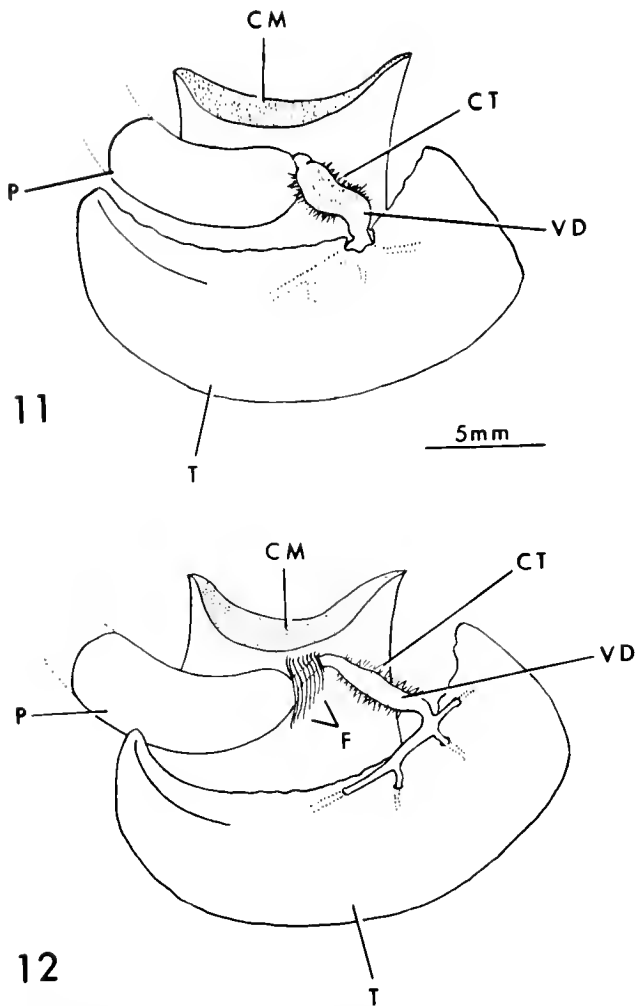
Clench and Fuller (1965) gave a partial history of the



Figures 6–8. Periostracal surface of body whorl of juvenile *Bellamyia*. **6.** *B. chinensis* from Black Pond, Connecticut. **7.** Same, Forest Park ponds, Springfield, Massachusetts. **8.** *B. japonica* from Lake Mohegan, Connecticut. Scale line = 0.5 mm. **Figures 9–10.** Radula (central and lateral teeth). **9.** *Bellamyia japonica*. **10.** *Bellamyia chinensis*. Scale line = 0.05 mm.

taxonomy and nomenclature of these species. As can be deduced from their account, the original descriptions of these species were essentially brief accounts of the adult shell with very little geographical data provided. Pace's (1973) review of the taxonomy of *B. chinensis* probably best summarizes the nomenclatural and taxonomic confusion that accompanies this species. Seemingly every race or form encountered by early workers was established on the most subtle of characters. Differences of opinion on the validity of named forms and generic as-

signment was quite likely compounded by difficulties in communication between Asian and European investigators. Unfortunately, the practice of naming new species of Asiatic viviparids on the basis of a few qualitative shell characters continues (Li, 1990; Liu *et al.*, 1994). Until future study requires otherwise, I follow Pace (1973) and other earlier workers who assert that many of the subsequently named forms related to *B. chinensis*, including *B. malleata*, are at most subspecies. Given that subspecific status is normally maintained through geographic



Figures 11–12. Anatomy of male reproductive structures. 11. *Bellamya chinensis*. 12. *Bellamya japonica*. Scale applies to figures 11 and 12. CM = columellar muscle, CT = connective tissue (mesentery), F = fibers of columellar muscle, P = prostate, T = testes, VD = vas deferens.

not genetic, separation, and that several populations of interbreeding *B. chinensis* have been introduced into North America, the features that defined any particular subspecies have most likely been obliterated. Furthermore, in that most opinion leans towards a Japanese origin for at least some of the North American populations and that populations of each species have been reported in Japan (Kuroda, 1929), I believe that *B. japonica* s. l. and *B. chinensis* s. l. are the species involved.

The decision to place both species with *Bellamya* results in part from Taylor's (1981) statement, substantiated by anatomical data provided in this study, that *B. japonica* belongs to the Bellamyinae. With respect to the continued use of the name *Cipangopaludina* for *B. chinensis*, those characters used to substantiate the genus are either variable or characteristic of animals reaching a relatively large size. Notwithstanding the absence of a carina on the adult shell, originally used by Hannibal

(1912) in his description, the foundation of *Cipangopaludina* lies chiefly in certain anatomical features discussed above. Folding of the gill filament, a character of *Cipangopaludina* established by Rao (1925), was not observed in either species. Folding of the filament may be caused by contraction or may represent distortion as a result of preservation. A thick mantle edge and a developed sphincter muscle are present in both species, but based on comparison with smaller *Viviparus georgianus* (I. Lea, 1834) thickness and muscle size can be related to animal size (Smith, pers. observ.). A comparison of mantle types illustrated by Annandale (1920: 112) and used to characterize *Lecythoconcha* (= *Cipangopaludina*) apart from other genera more clearly demonstrates a gradation of mantle development among the groups he discussed. In relation to brain complexity (sensu Rao, 1925), more detailed studies are necessary for the proper evaluation of this character. Following Rohrbach's (1937) anatomical system, which was somewhat extended by Pace (1973), *B. japonica* represents a group within *Bellamya* that is characterized by a branched vas deferens proximal to the testes; *Bellamya chinensis* represents a sister group that has an unbranched free portion of the vas deferens. Vail (1977) has addressed the problems of subgroups within *Bellamya* in a more general fashion and suggested that further studies are necessary to establish natural groups within the Bellamyinae. It is thus proposed that *Cipangopaludina* should be treated as a subgenus of *Bellamya*, a decision with some precedent. *Cipangopaludina* would provisionally embrace the large bellamyids with unbanded shells during any part of their life history and with native distributions limited to Asia.

ACKNOWLEDGMENTS

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A revision of the Patagonian genus *Xymenopsis* Powell, 1951 (Gastropoda: Muricidae)

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ABSTRACT

The genus *Xymenopsis* Powell, 1951 is revised and restricted to 4 Recent species: *Xymenopsis muriciformis* (King and Broderip, 1832), *X. corrugatus* (Reeve, 1848), *X. buccineus* (Lamarck, 1816) and *X. subnodosus* (Gray, 1839). Of the 34 nominal species that have been described as or assigned to *Xymenopsis* by various authors, 3 belong to the buccinid genus *Parreuthria* and 1 is a trophonine muricid not closely related to *Xymenopsis*. The taxonomic affinities of each of the remaining 30 names (one is a replacement name) are discussed. Eleven holotypes and ten lectotypes (nine newly designated) are illustrated, many for the first time. Types of 3 taxa were destroyed during World War II and another 5 types are lost. Neotypes are designated for *Fusus buccineus* Lamarck, 1816, the oldest name to be applied to any species of *Xymenopsis*, as well as for *Buccinum subnodosa* Gray, 1839, *Trophon brucei* Strebel, 1904, *Trophon fenestratus* Strebel, 1904, *Trophon paessleri turrita* Strebel, 1904, *Trophon ringei* Strebel, 1904 and *Trophon standeni* Strebel, 1904. This is done to remove any ambiguity regarding the identity of these taxa, and thus stabilize the nomenclature of Recent species of *Xymenopsis*. The gross anatomy and morphology of the radula, egg capsule, protoconch, and shell ultrastructure of the type species of *Xymenopsis* are described and illustrated. *Xymenopsis* is compared to, and differentiated from, the genera *Xymene*, which is restricted to New Zealand, and *Trophon*, with which it co-occurs in the Magellanic province.

Key words: Neogastropoda, Trophoninae, Patagonia, Magellanic Province.

INTRODUCTION

The genus *Xymenopsis* encompasses a group of small, conchologically variable muricid gastropods endemic to the Magellanic Province. These shell-drilling predators commonly co-occur with species of *Trophon* on mussel beds, and range from the intertidal zone to depths exceeding 100 meters. The majority of the published literature on this group dates from the early era of Antarctic and subAntarctic exploration, and has concentrated on describing numerous, minor phenotypic variants

as species. The biology of these animals has not previously been studied.

Powell (1951) erected the genus *Xymenopsis* to distinguish Patagonian muricids with a conical, multi-whorled protoconch and rounded axial ribs from those with a rounded, paucispiral protoconch and numerous, lamellose varices that belong to the genus *Trophon*. He attributed 30 nominal taxa to *Xymenopsis*, but recognized that many would prove to be synonyms, stating that "An evaluation of these names is not possible without recourse to the type material which is in European museums." Implicit in the generic name *Xymenopsis* is Powell's recognition of the close affinity of this Magellanic group to *Xymene* Iredale, 1915, which is endemic to New Zealand. Powell (1951) noted that the shell sculpture of *Xymenopsis* was similar to that of *Xymene*, but that its protoconch resembled that of *Zeatrophon* Finlay, 1927, another New Zealand genus.

In his revision of New Zealand muricids assigned to the genus *Trophon*, Finlay (1926) proposed several supraspecific taxa, each representing what he regarded to be a lineage or "natural grouping." He divided these taxa into 2 groups, based primarily on protoconch morphology. One group, defined on the basis of having a symmetrically conical protoconch of > 2 whorls and a small nucleus, contained the genera *Xymene* Iredale, 1915, *Xymenella* Finlay, 1926, and *Zeatrophon* Finlay, 1927. The second group, recognized by having an asymmetrical, rounded protoconch of 1–2 whorls, with a large, lateral nucleus, included *Axymene sensu stricto* Finlay, 1926, *Axymene* (*Lenitrophon*) Finlay, 1926, *Comptella* Finlay, 1926, *Terefundus sensu stricto* Finlay, 1926, and *Terefundus* (*Minortrophon*) Finlay, 1926.

Ponder (1972) reviewed the Recent and fossil New Zealand species related to *Xymene*. Based on an analysis of gross anatomy, shell, and radular morphology, he concluded that the taxa *Axymene*, *Lenitrophon*, *Xymenella*, *Zeatrophon*, and probably *Vesanula* Finlay, 1926, did not merit taxonomic recognition even at the subgeneric level, and reduced all but *Vesanula* to synonyms of *Xymene*. However, he regarded *Xymenopsis* sufficiently distinct to

Table 1. Taxa attributed to the genus *Xymenopsis* by Powell (1951) and Dell (1971, 1972). Taxa listed in **bold** are valid species.

| | |
|---|--|
| <i>Trophon acuminatus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon albus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus albidus</i> Philippi, 1845 | (synonym of <i>Xymenopsis buccineus</i>) |
| <i>Trophon brucei</i> Strebel, 1904 | (synonym of <i>Xymenopsis corrugatus</i>) |
| <i>Xymenopsis buccineus</i> (Lamarek, 1816) | |
| <i>Trophon cancellarioides</i> Reeve, 1847 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Xymenopsis cancellinus</i> (Philippi, 1845) | (synonym of <i>Xymenopsis subnodosus</i>) |
| <i>Fusus candidatus</i> Rochebrune and Mabille, 1889 | (belongs in the buccinid genus <i>Pareuthria</i> Strebel, 1905) |
| <i>Xymenopsis corrugatus</i> (Reeve, 1848) | |
| <i>Trophon couthouyi</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus decolor</i> Philippi, 1845 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus dispar</i> Rochebrune and Mabille, 1889 | (belongs to different muricid genus, not <i>Xymenopsis</i>) |
| <i>Trophon elegans</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon elongatus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon falklandicus</i> Strebel, 1908 | (synonym of <i>Xymenopsis corrugatus</i>) |
| <i>Trophon fenestratus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon hoylei</i> Strebel, 1904 | (synonym of <i>Xymenopsis corrugatus</i>) |
| <i>Fusus jacquiniti</i> Philippi, 1855 | (new name for <i>F. textilosus</i> Hombron and Jacquinot, 1854, not <i>F. textilosus</i> Deshayes, 1835) |
| <i>Fusus lebrunii</i> Mabille and Rochebrune, 1889 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus liratus</i> Gould, 1849 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus loebbeckei</i> Kobelt, 1878 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Xymenopsis muriciformis</i> (King and Broderip, 1832) | |
| <i>Trophon obesus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon ornatus</i> Strebel, 1904 | (synonym of <i>Xymenopsis corrugatus</i>) |
| <i>Trophon paessleri</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon paessleri turrita</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Fusus plumbeus</i> Gould, 1952 | (belongs in the buccinid genus <i>Pareuthria</i> Strebel, 1905) |
| <i>Trophon pseudoelongatus</i> Strebel, 1904 | (synonym of <i>Xymenopsis muriciformis</i>) |
| <i>Trophon ringei</i> Strebel, 1904 | (synonym of <i>Xymenopsis buccineus</i>) |
| <i>Fusus roseus</i> Hombron and Jacquinot, 1854 | (belongs in the buccinid genus <i>Pareuthria</i> Strebel, 1905) |
| <i>Trophon standeni</i> Strebel, 1904 | (synonym of <i>Xymenopsis corrugatus</i>) |
| <i>Xymenopsis subnodosus</i> (Gray, 1839) | |
| <i>Fusus textilosus</i> Hombron and Jacquinot, 1854 | (synonym of <i>Xymenopsis buccineus</i>) |
| <i>Fusus violaceus</i> Mabille and Rochebrune, 1889 | (synonym of <i>Xymenopsis muriciformis</i>) |

be treated as a subgenus of *Xymene*. Despite reducing their taxonomic rank, Ponder (1972) recognized 5 distinctive groups within the *Xymene* complex, corresponding to: 1) *Xymene* + *Xymenella*; 2) *Zeatrophon*; 3) a group consisting of 2 fossil species (1 Eocene, 1 Miocene) with features expected in the "ancestor of all the species of *Xymene*"; 4) *Axymene*; and 5) *Xymenopsis*.

Beu and Maxwell (1990:39) reported *Xymene* to range from the Kaiatan (= Bartonian, Late Eocene) to the Recent in New Zealand. The fossil record of *Xymenopsis* is thus far limited to 4 species recently described from the Late Miocene Entrerriense Formation along the Valdés Peninsula in northern Patagonia, Argentina (Brunet, 1997). While there is little doubt that *Xymene* and *Xymenopsis* are closely related, these lineages are treated here as separate genera.

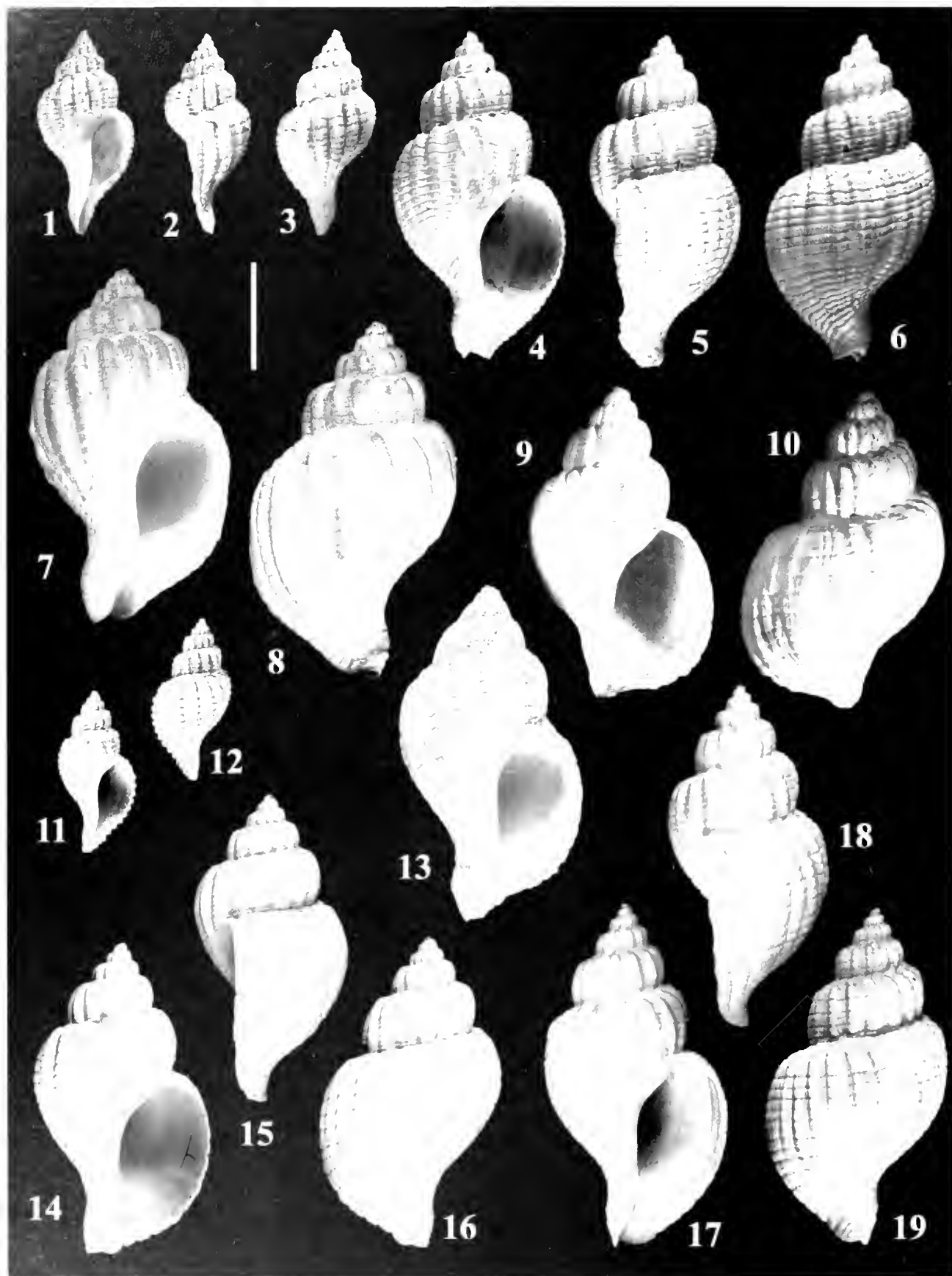
In the present study, we review and discuss all Recent nominal species that have been included in *Xymenopsis* (Table 1) based on an examination of available type material. Type specimens of all taxa referable to *Xymenopsis* that could be located are illustrated, some for the first time. Data on shell ultrastructure, radular morphology, and gross anatomy are provided for *Xymenopsis*

muriciformis, the type species of *Xymenopsis*. Comparative data are provided for *Xymene plebeius*, the type species of *Xymene*, and for the other Recent species of *Xymenopsis*.

MATERIALS AND METHODS

The majority of specimens examined in this study are in the collections of: the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Museo de La Plata, La Plata, Argentina (MLP); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN); and the Los Angeles County Museum of Natural History (LACM). Type material is housed in the following museums: The Natural History Museum, London, (BMNH); Zoologisches Institut und Zoologisches Museum der Universität Hamburg, (ZMH); Swedish Museum of Natural History, Stockholm, (NHRM); Museum national d'Histoire naturelle, Paris (MNHN); Museo Nacional de Historia Natural, Santiago, Chile (MNHNS); and, Loebbecke-Museum und Aquazoo, Dusseldorf, (LM).

Dissections were performed on ethanol preserved



specimens to study their gross anatomy, with emphasis on the morphology of the anterior alimentary system, and the pallial portions of the male and female reproductive systems. Radulae were prepared according to the method described by Solem (1972) and observed using a LEO 440 scanning electron microscope (SEM). Radular terminology follows Kool (1993a: fig. 6B). Shell ultrastructure data were procured from freshly fractured collabral sections taken from the central portion of the lip on the last whorl of 2 individuals per taxon, whenever sufficient material was available.

Most photographs were taken using a Leaf Lumina digital scanning camera. Several images were scanned from black and white 35 mm negatives using a Nikon Coolsan III slide scanner. All images were processed with the software Photoshop 4.01 and 5.02.

SYSTEMATICS

Class Gastropoda Cuvier, 1797

Order Neogastropoda Wenz, 1938

Family Muricidae Rafinesque, 1815

Subfamily Trophoninae Cossmann, 1903

Genus *Xymenopsis* Powell, 1951

Xymenopsis Powell, 1951:158; Radwin and D'Attilio, 1976:190.
Xymene (*Xymenopsis*) Ponder, 1972:474; Vokes, 1991:10.

Type species: *Fusus liratus* Gould, 1849 (by original designation), a junior synonym of *Buccinum muriciforme* King and Broderip, 1832.

Diagnosis: The genus *Xymenopsis* contains species characterized by a small to medium-sized (to 48 mm), fusiform, high-spired shell with a tall, conical, multi-whorled (≈ 3 whorls) protoconch that lacks a keel, and a teleoconch with a rounded shoulder, sculpture of rounded axial ribs that never develop lamellae, and narrow to broad spiral cords that may or may not produce beads at intersections with axial ribs. The siphonal canal is short, open, and broad. Shell ultrastructure consists of an outer amorphous calcitic layer and an inner, crossed-lamellar aragonitic layer. The rachidian tooth of the radula has a basal plate that is simple and concave anteriorly, and inner lateral denticles that are completely free from the central and lateral cusps. The mantle edge is always lobulated.

Remarks: In his treatment of the *Xymene* complex, Ponder (1972) identified the oldest known member of the group in the Late Eocene fauna of South Island, New Zealand. He recognized that *Xymene apipagodus*

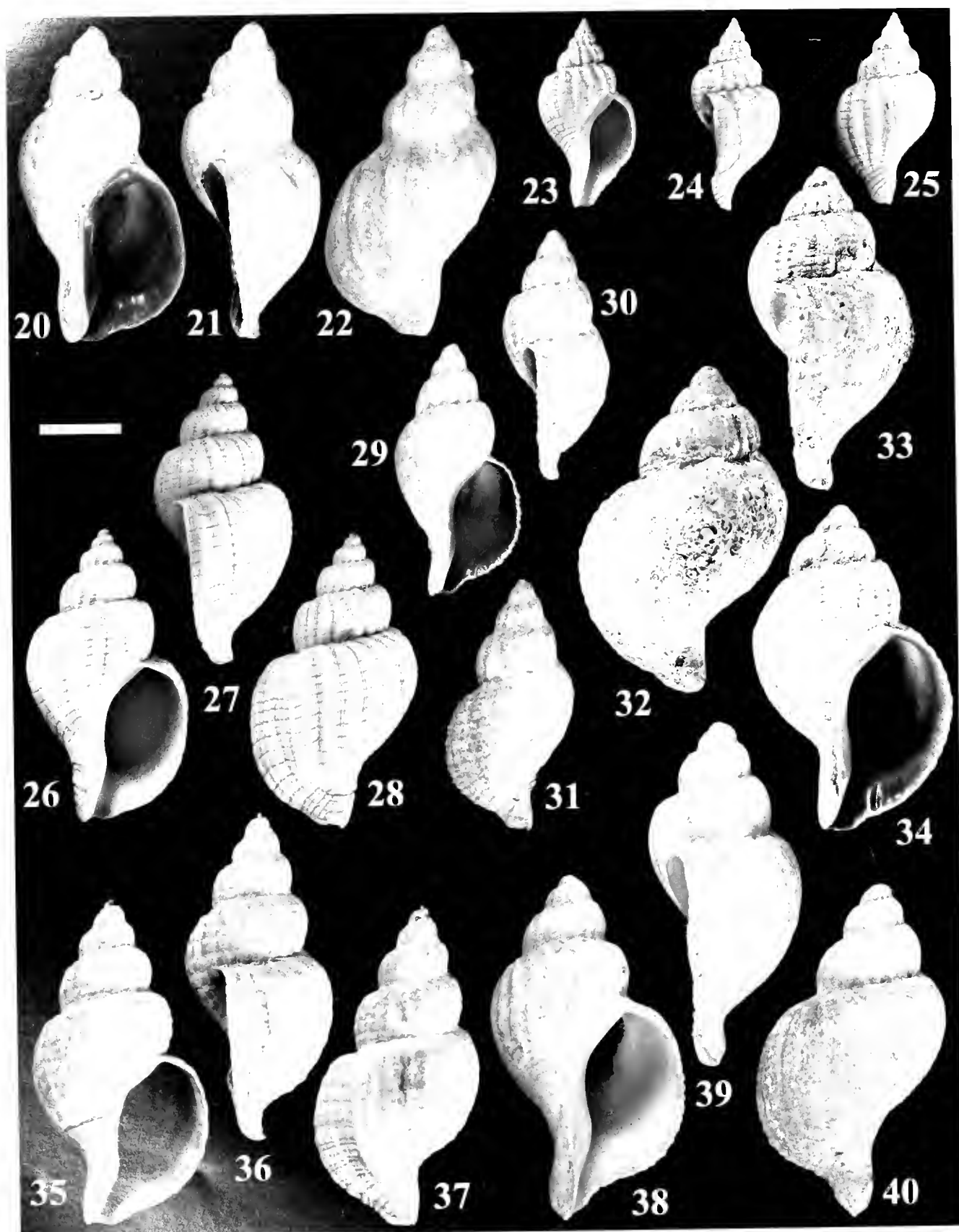
Ponder, 1972, characterized by a small, strongly shouldered shell with axial lamellae, smooth aperture, and a tall, conical, $4\frac{1}{2}$ -whorled protoconch with a sinuated varix indicative of a pelagic larval stage, had features from which all subsequent *Xymene* lineages could be derived, and suggested that several lineages evolved from this phenotype.

One lineage comprises the *Zeatrophon* group, which appeared during the Late Oligocene (*Xymene chattonensis* Ponder, 1972, Duntroonian) and persists in the Recent fauna (e.g., *Zeatrophon ambiguus* Finlay, 1927, the type species of *Zeatrophon*). This lineage is characterized by a tall, strongly shouldered shell with axial nodes or weak lamellae, an aperture with or without lirae, and a protoconch that is tall and conical, yet smaller and with fewer ($2\frac{3}{4}$ – $3\frac{3}{4}$) whorls than *X. apipagodus*. Within this lineage, there is a trend for a spiral keel to develop on the last protoconch whorl, and for the nucleus of the protoconch to increase in size. A second lineage (*Xymene* + *Xymenella* group) also appeared in the Late Oligocene (*Trophon lepidus* Suter, 1917, Duntroonian) and survives in the Recent fauna (e.g., *Fusus plebeius* Hutton, 1873, the type species of *Xymene*, and *Trophon pusillus* Suter, 1917, the type species of *Xymenella*). Shells are small, strongly to weakly shouldered, with strong spiral cords and axial ribs, but without lamellae, and with apertures that are usually lirate. Protoconchs are depressed, with a trend to fewer (2 whorls in *X. plebeius*, $2\frac{1}{2}$ whorls in *X. gouldi* = *T. pusillus*, see Ponder, 1972), more inflated whorls, and an increase in the size of the nucleus. Another lineage (*Axymene* group) is limited to Pliocene and Recent species. Shells tend to be large, strongly shouldered, with axial ribs and spiral cords, but without lamellae, and generally have lirate apertures. Protoconchs consist of 1–2 rounded, inflated whorls, with a large nucleus.

Beu *et al.* (1997) regarded *Xymene* and *Xymenella* to be distinct genera, and reassigned *Triton dautzenbergi* von Ihering, 1897, and *Urosalpinx elegans* Ortmann, 1900, both from the Monte León Formation (Late Oligocene–Early Miocene) of Patagonia, to *Xymene*, and *Xymenella* respectively. Based on the first occurrences of these taxa in the fossil record, they concluded that *Xymenella* originated in New Zealand and dispersed to South America with the origin of the Antarctic Circumpolar Current at the time the Drake Passage opened (Late Oligocene), while *Xymene* evolved in South America and dispersed to New Zealand, also along the Ant-

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Figures 1–19. *Xymenopsis muriciformis* (King and Broderip, 1832). **1–3.** Holotype of *Fusus liratus* Gould, 1849, USNM 5680, Orange Harbor, Tierra del Fuego. **4–6.** Holotype of *Trophon loebbeckei* Kobelt, 1878, Loebbecke Museum unnumbered, lacks locality data. **7–8.** Lectotype of *Trophon violaceus* Mabilie and Rochebrune, 1889, MNHN unnumbered, Baie Orange, Tierra del Fuego. **9–10.** Holotype of *Fusus decolor* Philippi, 1845, MNHN unnumbered, Strait of Magellan. **11–12.** Lectotype of *Trophon elegans* Strebel, 1904, ZMH unnumbered, Port Stanley, Malvinas (Falkland) Is. **13.** Lectotype of *Trophon lebruni* Mabilie and Rochebrune, 1889, MNHN unnumbered, Santa Cruz, Argentina. **14–16.** Lectotype of *Buccinum muriciforme* King and Broderip, 1832, BMNH 1837.12.15.2695, Strait of Magellan. **17–19.** Lectotype as *Buccinum cancellarioides* Reeve, 1847, BMNH 1992055, lacks locality data. Scale bar = 1 cm for all specimens.



arctic Circumpolar Current, during the Middle Miocene.

The origin of the *Xymene* complex in New Zealand is amply supported by the fossil record. The hypothesized dispersal of this lineage to Southern South America during the Late Oligocene is concordant with its appearance in the fossil record of the region, and is supported by the prevalence of narrow, polygyrate protoconchs, indicative of pelagic larval stage (see Thorson, 1950; Shuto, 1974; Jablonsky and Lutz, 1980), in Paleogene members of this complex. Recent and fossil species of *Xymenopsis* are most similar to members of the *Xymene* + *Xymenella* group, especially to early members of this lineage such as the Oligocene *Xymene lepidus*, with which they share a sculptural pattern of axial ribs and spiral cords, but not axial lamellae, and a conical, 3 whorled protoconch with a small, apical nucleus. We suggest that *Xymenopsis* represents a radiation endemic to the Magellanic region from ancestors of the *Xymene* + *Xymenella* group that dispersed as larvae to Patagonia during the Late Oligocene.

While it is possible that multiple lineages were introduced to South America, or that 1 lineage subsequently dispersed back to New Zealand while becoming extinct in South America, evidence for such hypotheses is more tentative or lacking. *Xymene* are characterized by a trend to protoconchs with fewer, more rounded whorls that are indicative of lecithotrophic rather than planktotrophic development. This would argue against their ability to disperse as planktonic larvae from South America eastward on the Antarctic Circumpolar Current to New Zealand. Clearly, a rigorous re-assessment of the *Xymene* complex in a phylogenetic context would resolve many of the systematic and biogeographic questions that have plagued this group.

Xymenopsis lack the strongly shouldered shell of the *Xymene* + *Xymenella* group. While strong apertural lirae are prevalent in *Xymene*, they are rare in *Xymenopsis*, occurring only in the *X. subnodosus* (Gray, 1839). *Xymenopsis* may also be distinguished from *Xymene* on the basis of shell ultrastructure, radular morphology and by features of their mantle edge and egg capsules. *Xymenopsis* (figures 45, 79, 80) has a thick ($> \frac{1}{2}$ shell thickness) outer layer of calcite, and a single layer of crossed-lamellar aragonite in which the crystal faces are comarginal. In *Xymene* (figure 50), the calcitic layer is thin, the co-marginal layer of aragonite thickest, and an innermost layer of crossed-lamellar aragonite, with crystal faces perpendicular to those of the co-marginal layer, is

also present. The radula of *Xymene plebeius* has rachidian teeth (figure 51) that are characteristically chevron-shaped, each with its apex at the mid-point of the anterior edge of the basal plate, which has a concave posterior edge. Rachidian teeth of *Xymenopsis* (figures 48–49, 75–76, 81–82, 102–103) have a straight to slightly concave anterior edge, and a convex posterior edge of the basal plate. The mantle edge of *Xymene* is smooth, while the mantle edge of *Xymenopsis* is lobulated. While egg capsules of *Xymene* (figure 43) and *Xymenopsis* (figure 42) are similar, the exit aperture is apical in *Xymene*, but is situated at the base of a shallow depression in *Xymenopsis*.

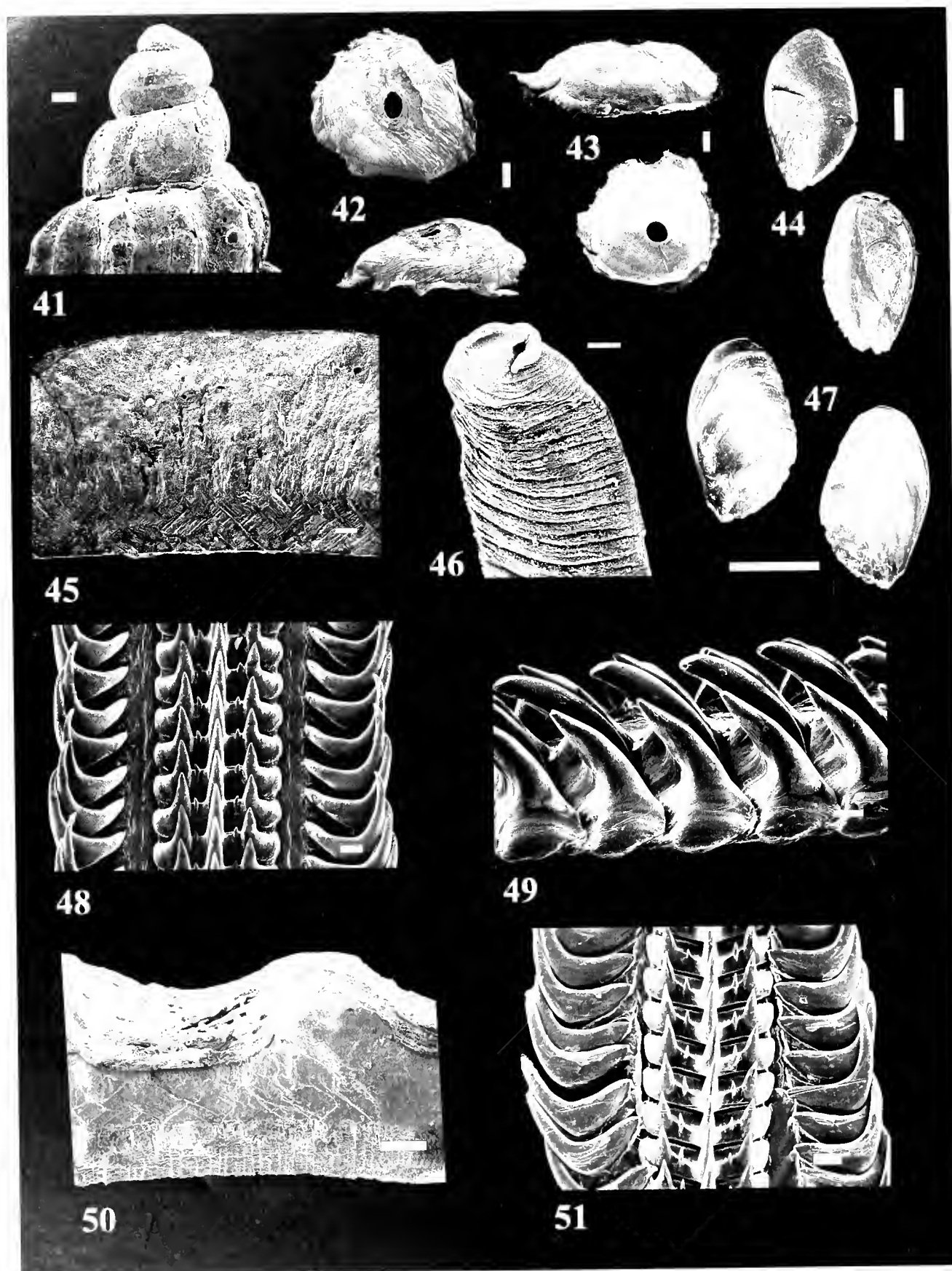
There are no direct observations on development in *Xymenopsis*. Shuto (1974) reported that the ratio of the protoconch diameter (D) to the number of whorls (V) is a reasonable estimator of the type of development, and that a ratio below 0.3 is characteristic of planktotrophic larvae, especially when the number of whorls is ≥ 3 . Both *Xymenopsis muriciformis* (figure 41) and *X. buccineus* (figures 77–78) have narrow, conical protoconchs of 3 whorls. The D/V ratios for these species are 0.23 and 0.21 respectively, predicting that, unlike *Xymene*, *Xymenopsis* retains planktotrophic larval development.

Powell (1951) provisionally included the species *Fusus roseus* Hombron and Jacquinot, 1854 and *Trophon candidatus* Rochebrune and Mabile, 1889 in his genus *Xymenopsis*. Cernohorsky (1977) subsequently transferred *Fusus roseus* to the buccinid genus *Paranthuria* Strebel, 1905. He proposed the new name *Paranthuria powelli* for this species because *Fusus roseus* Hombron and Jacquinot, 1854 was preoccupied by *Fusus roseus* Anton, 1838. The type material of these taxa was examined by the senior author at the Museum national d'Histoire naturelle, and both are clearly referable to the buccinid genus *Paranthuria*. The type material of *Fusus dispar* Hombron and Jacquinot, 1854 was also examined (MNHN). This taxon has affinities with the Antarctic Trophoninae, but does not belong to the genus *Xymenopsis*.

Xymenopsis muriciformis (King and Broderip, 1832)
(Figures 1–42, 45–49, 83–95, 105–106)

Buccinum muriciforme King and Broderip, 1832:348.
Fusus muriciformis King and Broderip—Gray, 1839:118.
Fusus buccineus Sowerby in Gray, 1839:155, pl. 36, fig. 12.
Fusus decolor Philippi, 1845:68, 1846:118, pl. 3, fig. 3; Hupé

Figures 20–40. *Xymenopsis muriciformis* (King and Broderip, 1832). **20–22.** Holotype of *Trophon acuminatus* Strebel, 1904, ZMH unnumbered, Punta Arenas, Strait of Magellan. **23–25.** Lectotype of *Trophon couthouyi* Strebel, 1904, ZMH unnumbered, Port Grappler, Smyth Channel. **26–28.** Lectotype of *Trophon paessleri* Strebel, 1904, (specimen coated with ammonium chloride), ZMH unnumbered, Port Grappler, Smyth Channel. **29–31.** Holotype of *Trophon pseudolongatus* Strebel, 1904, ZMH unnumbered, Ushuaia. **32–34.** Lectotype of *Trophon obesus* Strebel, 1904, ZMH unnumbered, Punta Arenas, Chile. **35–37.** Lectotype of *Trophon elongatus* Strebel, 1904, ZMH unnumbered, Puerto Augusto, Strait of Magellan. **38–40.** Holotype of *Trophon albus* Strebel, 1904, ZMH unnumbered, Ushuaia. Scale bar = 1 cm for all specimens.



in Gay, 1854:162; Hombron and Jacquinot in Rousseau, 1854:108, pl. 25, figs. 6–8; Kobelt, 1878:291, pl. 74, figs. 5–6; Rochebrune and Mabilie, 1889: H.54.
Buccinum cancellarioides Reeve, 1847:pl. 14, fig. 113.
Fusus liratus Gould, 1849:141.
Trophon liratus Couthouy—Kobelt, 1878:310; Tryon, 1880:143, pl. 31, fig. 333; Watson 1886:165; Lamy, 1906:3.
Trophon Loebbeckei Kobelt, 1878:294, pl. 74, figs. 13, 14; Tryon, 1880:145, pl. 31, fig. 335.
Trophon muriciformis King—Tryon, 1880:145.
Trophon lebruni Mabilie and Rochebrune in Rochebrune and Mabilie, 1889: H.55.
Trophon violaceus Mabilie and Rochebrune in Rochebrune and Mabilie, 1889: H.56, pl. 2, fig. 1.
Trophon paessleri Strebel, 1904:213, pl. 7, figs. 56a–f.
Trophon paessleri var. *turrita* Strebel, 1904:215, pl. 7, fig. 57.
Trophon elongatus Strebel, 1904:217, pl. 7, figs. 58a–f.
Trophon pseudolongatus Strebel, 1904:220, pl. 7, figs. 60a,b.
Trophon albus Strebel, 1904:221, pl. 7, fig. 61.
Trophon acuminatus Strebel, 1904:222, pl. 7, fig. 63.
Trophon obesus Strebel, 1904:223, pl. 7, fig. 62.
Trophon fenestratus Strebel, 1904:225, pl. 7, fig. 59a–d.
Trophon couthouyi Strebel, 1904:236, pl. 7, fig. 65a–e; Pl. 8, fig. 76.
Trophon elegans Strebel, 1904:241, pl. 8, fig. 71.
Xymenopsis liratus (Gould)—Powell, 1951:158; Radwin and D'Attilio, 1976:190, fig. 136.
Xymenopsis decolor (Philippi)—Dell, 1971:211.
Xymenopsis muriciformis (King and Broderip)—Dell, 1972:8, figs. 31, 32; Vokes, 1991: 7, unnumbered fig.; Vokes, 1992: 3, figs. 5a–c; Castellanos and Landoni, 1993:16, pl. 3, figs. 39, 40C, D.

Diagnosis: Axial sculpture of irregular, rounded ribs, 16–20 on body whorl. Spiral sculpture of flat cords (4–6 on early whorls, 14–20 on body whorl), much broader than intervening spaces, which appear as incised furrows.

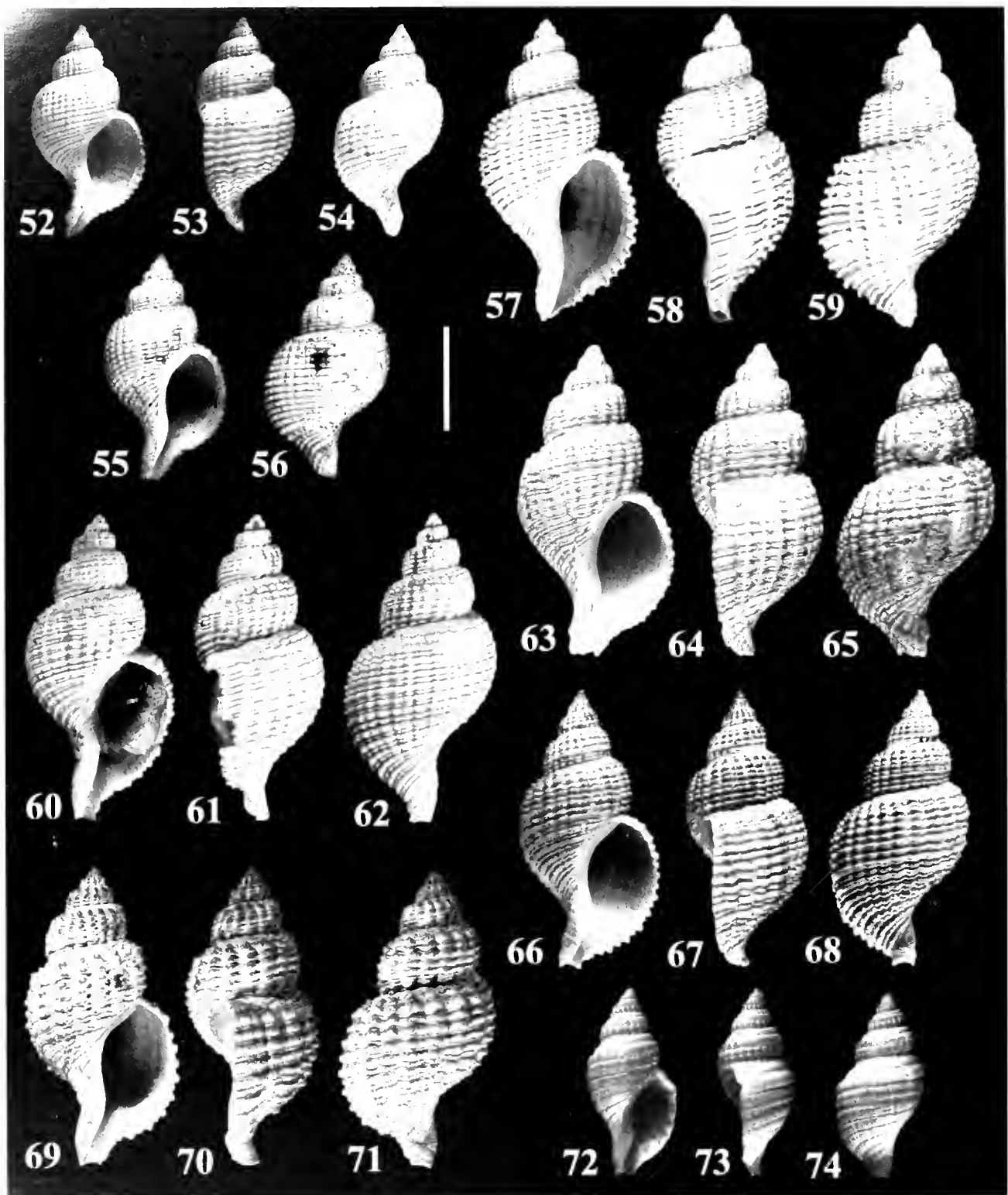
Description: Shell large for genus (reaching 48 mm), fusiform, slender, chalky. Protoconch of 3 tall, conical, whorls. Teleoconch of up to 6 weakly shouldered or rounded whorls. Spire high, $\approx \frac{1}{2}$ shell length, spire angle $\approx 45^\circ$. Suture deeply impressed; subsutural ramp narrow in early whorls, then absent. Aperture subovoid; outer lip rounded, anterior half-reflected; inner lip curved, adpressed; interior glossy pinkish to brownish. Siphonal canal short ($< \frac{1}{2}$ aperture length), oblique, open. Umbilicus absent. Axial sculpture of irregular, rounded ribs, 16–20 on body whorl. Spiral sculpture of flat cords (4–6 on early whorls, 14–20 on body whorl),

much broader than intervening spaces, which appear as incised furrows. Growth lines irregular, faint to obsolete throughout shell. Shell composed of 2 layers: outer layer thick (0.65 shell thickness), of amorphous calcite; inner layer (0.35 shell thickness), of crossed-lamellar aragonite with crystal planes oriented perpendicular to growing edge. Operculum (figure 47) oval, subpolygonal, with terminal nucleus. External surface covered by irregular growth lines. Inner surface with 3–4 horseshoe-shaped lines; posterior rim with slight callus, glazed in adult and young specimens.

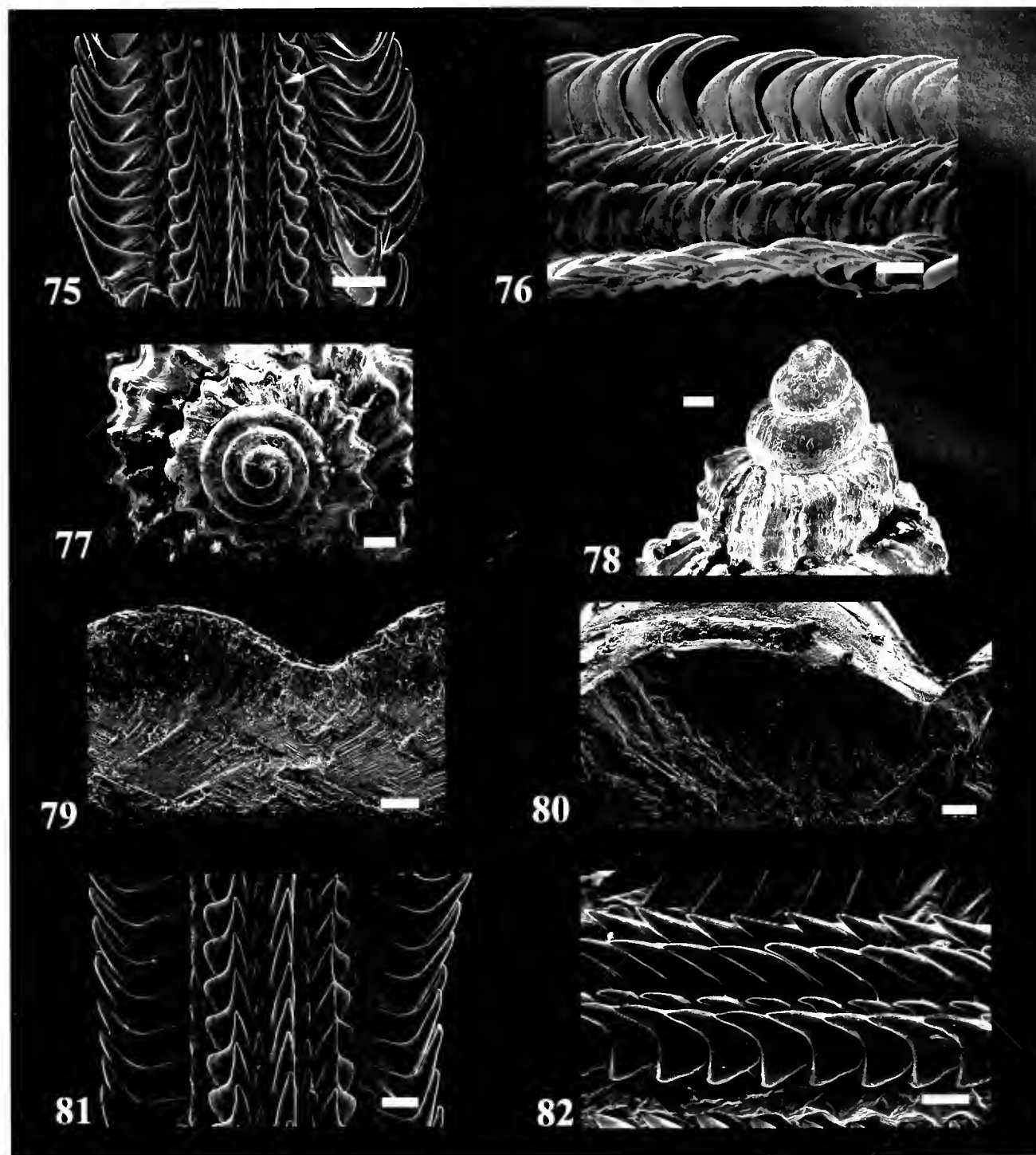
Animal large. Cephalic tentacles medium in size, blunt, thick, with small black eyes. Mantle edge with flat, rounded lobules (figure 83, l). Siphon (figure 83, s) of medium length. Accessory boring organ (figure 95, abo) situated along ventral midline of foot, shares opening with ventral pedal gland in females. Osphradium (figure 84, os) $< \frac{1}{2}$ ctenidium length, thin, very asymmetrical, with 45–50 leaflets per side. Ctenidium (figure 84, ct) 3–4 times as wide as osphradium, with 120–135 triangular leaflets. Pleuroembolic proboscis very long, broad. Radular ribbon (figures 48–49) small, short ($0.31 \times$ aperture length vs. $0.78 \times$ aperture length in *Trophon geversianus*), extends just beyond rear of buccal mass (figure 94, ra). Rachidian tooth wide (to $230\mu\text{m}$), central cusp large, needle-shaped, lateral cusps outwardly pointed, shorter than central cusp, inner lateral denticle small, thin, separate from lateral cusps. Basal plate of rachidian tooth rectilinear or gently curved, with low, broad, marginal areas. Lateral teeth large, each with single, long, scythe-shaped cusp and broad basal plate. Salivary glands (figure 94, sg), ascinous, white (yellow in fixed animals) very large, flanking retracted proboscis. Salivary ducts join esophagus just anterior to valve of Leiblein (figure 94, vl). Accessory salivary glands (figure 94, asg) small, pyriform, white to brownish, situated below salivary glands. Glande frambois  e absent. Gland of Leiblein (figure 94, gl) large, broad anteriorly, tapering posteriorly to form long, sinuous, blind duct with small, terminal ampulla (figure 94, dgl). Anterior aorta (figure 94, aa) passes through fold in gland of Leiblein en route to buccal mass. Stomach (figure 94, sto, 89) U-shaped, small, almost completely enveloped by digestive gland. Both digestive gland ducts (figure 89, dd) near esophageal opening, situated in deep pouch (figure 89, dp), separated from posterior mixing area (figure 89, pma) by small horizontal fold (figure 89, hf). Two typhlosoles (fig-

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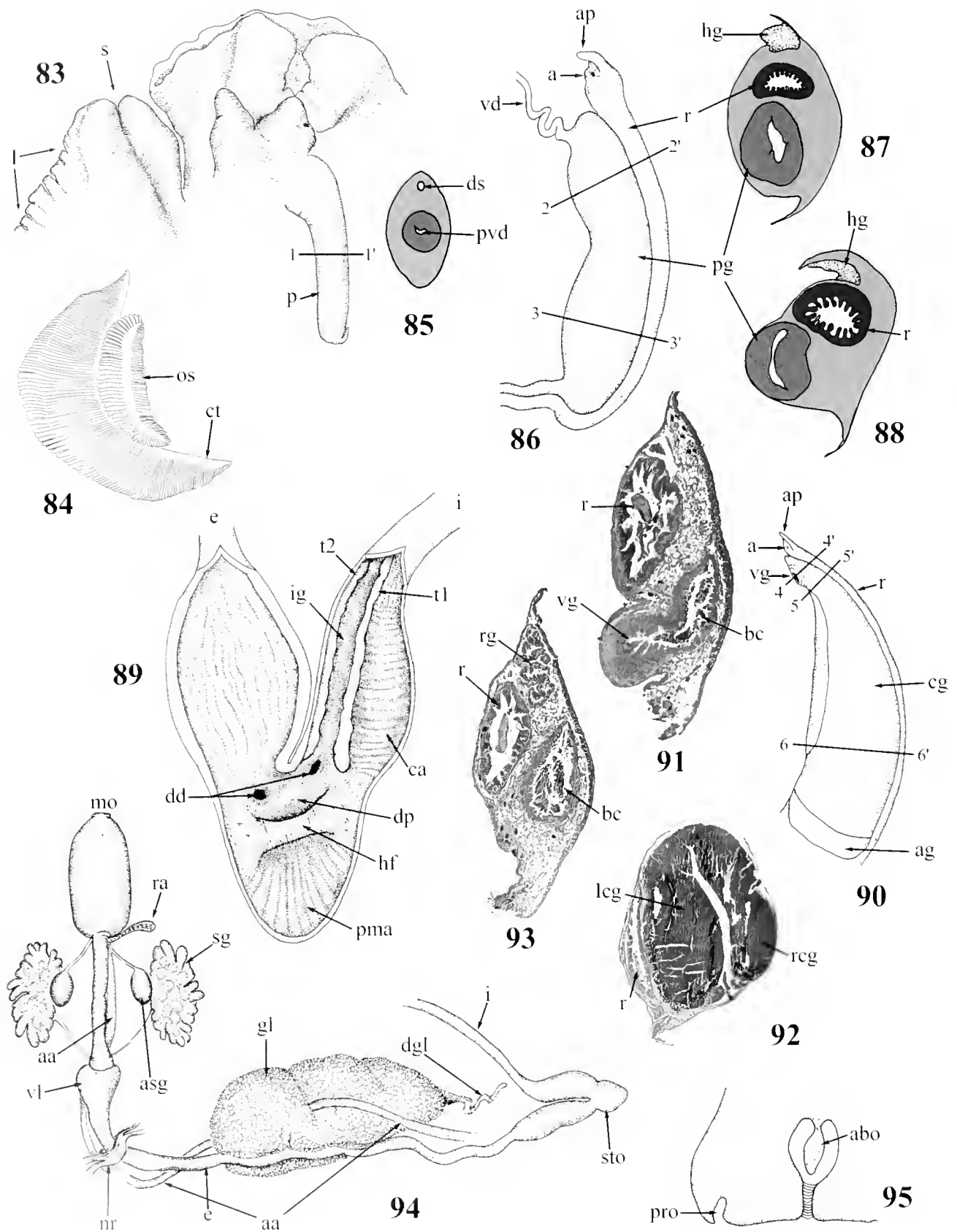
Figures 41–42, 45–49. *Xymenopsis muriciformis* (King and Broderip, 1832). **41.** Protoconch, USNM 901629, Strait of Magellan, $53^\circ 39.4'S$ – $70^\circ 55.5'W$, in 24 m. Scale bar = $100\mu\text{m}$. **42.** Apical and lateral views of the egg capsule. Scale bar = $800\mu\text{m}$. **45.** Shell ultrastructure, fracture surface comarginal. Scale bar = $30\mu\text{m}$. **46.** Penis, critical-point dried. Scale bar = $40\mu\text{m}$. **47.** Operculum, external (left) and internal (right) views. Scale bar = 1 cm. **48–49.** Radula USNM 901635, Strait of Magellan, $53^\circ 39.8'S$ – $70^\circ 54.9'W$, in 27–73 m. **48.** Dorsal view of radular ribbon. Scale bar = $40\mu\text{m}$. **49.** Lateral view of rachidian teeth. Scale bar = $20\mu\text{m}$. **Figures 43–44, 50–51.** *Xymene plebeius* (Hutton, 1873). **43.** Lateral and apical views of egg capsule, USNM 681538, Spit Beach, Dunedin Harbor, New Zealand. Scale bar = 1 mm. **44.** Operculum, external (left) and internal (right) views, same specimen as 43. Scale bar = 1 cm. **50.** Shell ultrastructure, fracture surface comarginal. AK 80295, Northland, Bay of Islands, Parekuta Bay, New Zealand. Scale bar = $100\mu\text{m}$. **51.** Dorsal view of radular ribbon, same specimen as 43. Scale bar = $20\mu\text{m}$.



Figures 52–56. *Apicunopsis buccinatus* Lamarck, 1816. 52–54, Neotype of *Fusus buccinatus* Lamarck, 1816, USNM 570410, 53°52'S, 64°57'W in 119–124 m. 55–56, Holotype of *Fusus textulosus* Hombron and Jacquinot, 1854, MNHN unnumbered, Strait of Magellan. Figures 57–71. *Apicunopsis corrugatus* Reeve, 1845. 57–59, Holotype of *Fusus corrugatus* Reeve, BMNH 1874.12.11.153, lacks locality data. 60–62, Lectotype of *Trophon hoyleri* Strebel, 1904, ZMH unnumbered, Port Stanley, Malvinas, Falkland Is. 63–65, Holotype of *Trophon falklandicus* Strebel, 1908, NHRM 1049, 51°35'S–57°56'W, Islas Malvinas, Falkland Is. 66–68, USNM 368350, Port Stanley, Malvinas, Falkland Is. 69–71, Holotype of *Trophon ornatus* Strebel, 1904, ZMH unnumbered, Port Stanley, Malvinas, Falkland Is. Figures 72–74. *Apicunopsis plebeius* Hutton, 1873, USNM 681538, Spit Beach, Dunedin Harbor, New Zealand. Scale bar = 1 cm for all specimens.



Figures 75–79. *Xymenopsis buccinatus* (Lamarck, 1816). **75.** Dorsal view of radular ribbon from specimen in figures 52–54. Scale bar = 40 μ m. **76.** Oblique (45°) lateral view of radular ribbon, MACN 12553, Tierra del Fuego. Scale bar = 40 μ m. **77–78.** Protoconch, MACN 25012, 54°26'S–64°53'W, in 112 m. **77.** Apical, and **78.** lateral views. Scale bars = 180 μ m. **79.** Shell ultrastructure, fracture surface comarginal. Scale bar = 40 μ m. **Figures 80–82.** *Xymenopsis corrugatus* (Reeve, 1848). **80.** Shell ultrastructure, fracture surface comarginal. USNM 368350, Port Stanley, Malvinas (Falkland) Is. Scale bar = 40 μ m. **81–82.** Radula USNM 421884, Port Williams, York Bay, Malvinas (Falkland) Is. **81.** Dorsal, and **82.** oblique lateral view. Scale bars = 20 μ m.



ure S9, t1, t2) flank intestinal groove (figure S9, ig) separating it from expanded compacting area (figure S9, ca). Intestine (figures S9, 94, i) runs anteriorly alongside pallial gonoduct, forming rectum with cylindrical papilla (figures S6, 90 ap) over anus (figures S6, 90 a). Rectal gland (figure 93, rg) small, inconspicuous, confined to anterior region of rectum. Prostate gland (figures S6–S8, pg) runs alongside rectum in mantle cavity, lacking openings to mantle cavity (unlike *Trophon geversianus*, see Kool, 1993b: fig. 57). Vas deferens (figure S6, vd) leads from anterior end of prostate to base of penis (figures 46, S3, p). Penis large ($> 3 \times$ tentacle length), wide, elongate, flattened to semitriangular in cross-section, with centrally situated sperm duct (figure S5, pvd), dorsal blood sinus (figure S5, ds). Penis tapers abruptly to form small, cylindrical papilla (figures 46, S3). Pallial oviduct broad posteriorly, tapered anteriorly. Albumen gland (figure 90, ag) situated at rear of mantle cavity, joins posterior of capsule gland (figure 90, cg). Left and right lobes of capsule gland similar to *T. geversianus* (Harasewych, 1984: fig. 22; Kool, 1993b), *Nuccella lapillus* (Fretter and Graham, 1994: fig. 171), but ventral and dorsal glandular areas proportionally much smaller (figure 92). Bursa copulatrix (figures 91, 93, bc) joins anterior of capsule gland, leads to vaginal opening (figures 90, 91, vg), situated below, posterior to anal opening, papilla (figure 90).

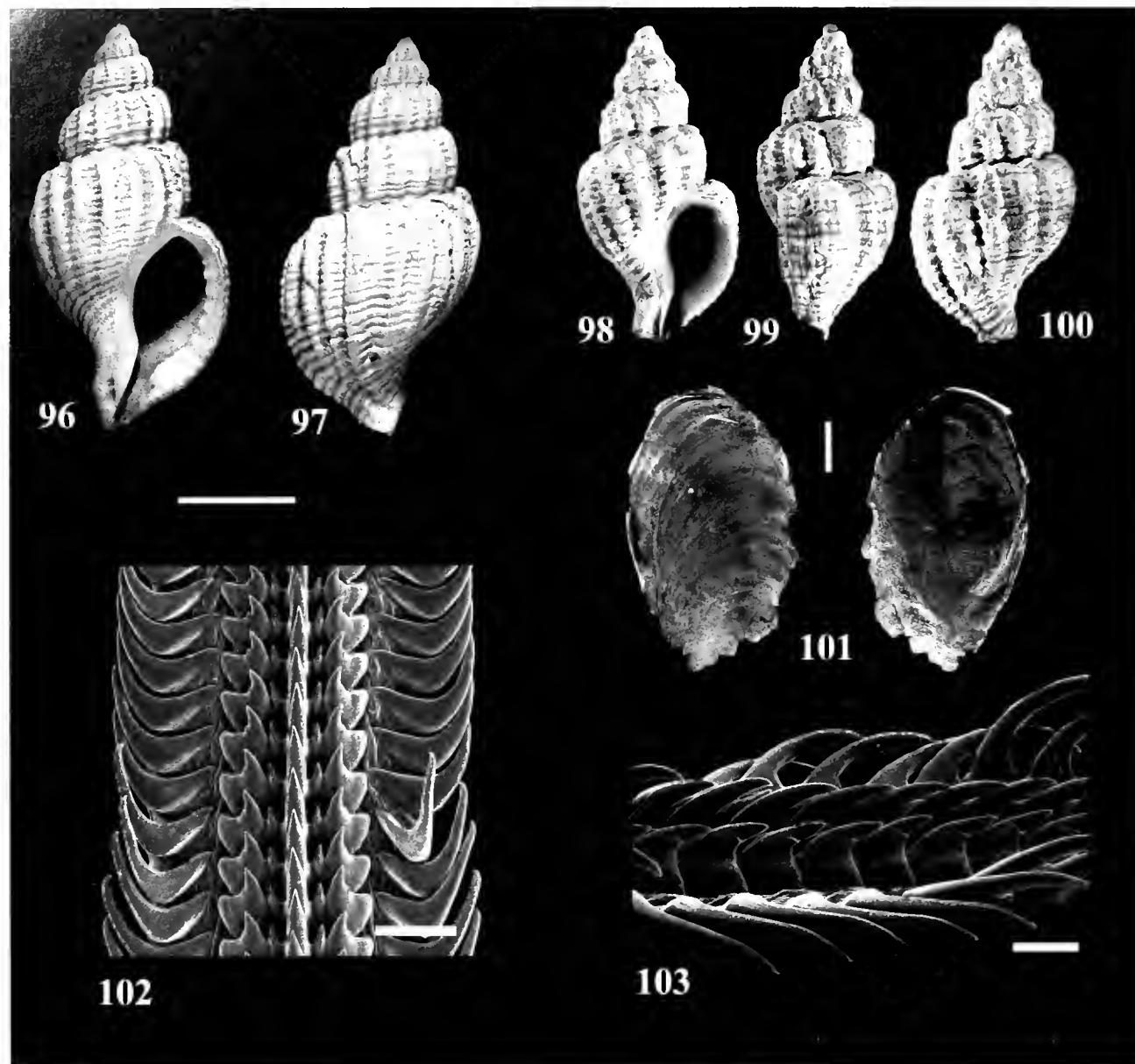
Egg capsules of *Xymenopsis muriciformis* were discussed but not illustrated by D'Asaro (1991:54). Capsules are attached to the dorsal surface of empty shells of *X. muriciformis*, densely grouped, overlapping each other. Egg capsule (figure 42) bulliform, approximately 6–7 mm in diameter, 2 mm high, outline subcircular, may vary according to substrate. Preformed exit aperture oval, situated at center of dorsal surface in shallow, sub-ovate depression, sealed by a mucus plug until hatching. Suture between capsule, plug weakly defined, running parallel to large axis of depression. Pattern of non-concentrically oriented fibers visible on upper surface of capsules. External morphology of egg capsules very similar to that observed in dry specimens of *Xymene plebeius* (figure 43), which differ in having aperture situated apically rather than in depression.

Type material: [*Buccinum muriciforme*] Lectotype (figures 14–16), BMNH 1837.12.15.2695, 6 paralectotypes, BMNH 1992056, all from Strait of Magellan; [*Fusus decolor*] Holotype (figures 9–10), MNHNS unnumbered, Strait of Magellan; [*Buccinum cancellarioides*] Lectotype (figures 17–19), BMNH 1992055-1, here designated, 1 paralectotype BMNH 1992055-2, lack locality data; [*Fusus livatus*] Holotype (figures 1–3), USNM 5680, Orange Harbor, Tierra del Fuego; [*Trophon lobbeckei*] Holotype (figures 4–6), Lobbecke-Museum, no catalog number, lacks locality data; [*Trophon lebruni*] Lectotype (figure 13), MNHN unnumbered, here designated, 2 paralectotypes, all from Santa Cruz, Argentina; [*Trophon violaceus*] Lectotype (figures 7–8), MNHN unnumbered, figured syntype here designated as lectotype, from Baie Orange, Tierra del Fuego; [*Trophon paessleri*] Lectotype (figures 26–28), ZMH unnumbered, here designated, 4 paralectotypes, all from Port Grappler, Smyth Channel, Strait of Magellan; [*Trophon paessleri* var. *turrita*] Original type material, from Cape Horn, Tierra del Fuego, was destroyed (Hansdorf *in litt.*). The lectotype of *Buccinum muriciforme* (BMNH 1837.12.15.2695) is here designated as neotype of *Trophon paessleri* var. *turrita*; [*Trophon elongatus*] Lectotype (figures 35–37), ZMH unnumbered, here designated, from Puerto Angosto, Strait of Magellan, 4 paralectotypes, 1 from Navarino Is., Chile, 1 from Puerto Bueno, 1 from Eden Harbor, 1 from Puerto Angosto, Strait of Magellan; [*Trophon pseudolongatus*] Holotype (figures 29–31), ZMH unnumbered, Ushuaia; [*Trophon albus*] Holotype (figures 38–40), ZMH unnumbered, Ushuaia; [*Trophon acuminatus*] Holotype (figures 20–22), ZMH unnumbered, Punta Arenas, Strait of Magellan; [*Trophon obesus*] Lectotype (figures 32–34), ZMH unnumbered, here designated, from Punta Arenas, Chile, 1 paralectotype from Punta Arenas, Chile; [*Trophon fenestratus*] Original type material, from Gregory Bank, Strait of Magellan, was destroyed (Hansdorf *in litt.*). The lectotype of *Buccinum muriciforme* (BMNH 1837.12.15.2695) is here designated as neotype of *Trophon fenestratus*; [*Trophon couthouyi*] Lectotype (figures 23–25), ZMH unnumbered, here designated, 4 paralectotypes, all from Port Grappler, Smyth Channel;

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Figures 83–95. *Xymenopsis muriciformis* (King and Broderip, 1832). **83.** Anterior portion of male specimen, mantle reflected. **84.** Ctenidium and osphradium. **85.** Transverse section of the penis. (figure 83 at 1–1'). **86.** Male pallial gonoduct. **87.** Transverse section (figure S6 at 2–2'). **88.** Transverse section (figure S6 at 3–3'). **89.** Stomach, opened dorsally. **90.** Female pallial gonoduct. **91.** Transverse section through capsule gland (figure 90 at 4–4'). **92.** Transverse section (figure 90 at 6–6'). **93.** Transverse section through bursa copulatrix (figure S4 at 5–5'). **94.** Diagrammatic representation of the alimentary system. **95.** Sagittal section through the anterior portion of the foot.

a = anus; aa = anterior aorta; abo = accessory boring organ; ag = albumen gland; ap = anal papilla; asg = accessory salivary gland; bc = bursa copulatrix; ca = compacting area; cg = capsule gland; ct = ctenidium; dd = ducts to digestive diverticula; dgl = ampulla of gland of Leiblein; dp = duct pouch; ds = dorsal blood sinus; e = esophagus; gl = gland of Leiblein; hf = horizontal fold; hg = hypobranchial gland; i = intestine; ig = intestinal groove; l = lobes along mantle edge; leg = left lobe of capsule gland; mo = mouth; nr = nerve ring; os = osphradium; p = penis; pg = prostate gland; pma = posterior mixing area; pro = propodial groove; pvd = penial vas deferens; r = rectum; ra = radula; reg = right lobe of capsule gland, rg = rectal gland; s = siphon; sg = salivary gland; sto = stomach; t1 and t2 = typhlosoles; vd = vas deferens; vg = vagina; vl = valve of Leiblein.

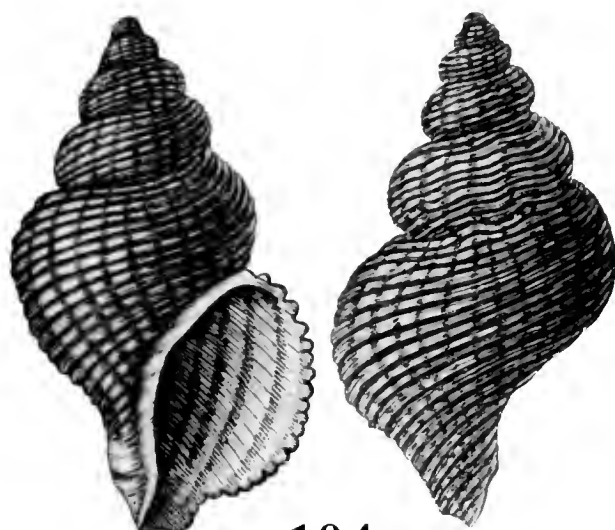


Figures 96–103. *Xymenopsis subnodosus* (Gray, 1839) **96–97.** Holotype of *Fusus cancellinus* Philippi, 1845, and neotype of *Buccinum subnodosa* Gray, 1839, MNHN unnumbered, Strait of Magellan **98–100.** BMNH 19990330, 43°38.9'17"S, 73°37'2'38"W **101.** Operculum, external (left) and internal (right) views, same specimen of 98–100. Scale bar = 1 cm **102.** Dorsal view of radular ribbon from specimen in figures 98–100. Scale bar = 50 μ m. **103.** Oblique (45°) lateral view, of radular ribbon. Scale bar = 25 μ m

[*Trophon elegans*] Lectotype (figures 11–12), ZMH unnumbered, here designated, from Port Stanley, Malvinas (Falkland) Is., 2 paralectotypes from Port Stanley, Malvinas (Falkland) Is.

Additional material examined: AMNH 50211, Strait of Magellan; AMNH 55425, Cañadón de las Vacas; AMNH 99610, West Malvinas (Falkland) Is.; AMNH 137057, Beagle Channel; AMNH 179293, Puerto Deseado; AMNH 271757, 53°37'7"S, 69°54.6'W, in 42 m; AMNH 271758, 54°10.2'S, 65°57.5'W, in 101 m; MACN

10043-1, Ushuaia; MACN 12374, Punta Arenas; MACN 12376, 53°10'S, 70°55'W; MACN 12448, Puerto Harris, Dawson Is.; MACN 12552, Río Grande; MACN 12555, Río del Fuego, Tierra del Fuego; MACN 13120, Punta Arenas; MACN 13568, Ushuaia; MACN 13569, Ushuaia; MACN 17754, Puerto Deseado; MACN 22567, Punta Colnet, Isla de los Estados; MACN 22717, 54°48'S, 64°55'W, in 103 m; MACN 23943, 20°07'S, 66°33'W, in 52 m; MACN 30876, Lapataia, Tierra del Fuego; USNM 96228, Strait of Magellan; USNM 96842, Puerto Mayne,



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Figure 104. Original illustration of *Fusus buccineus* Lamarck, 1816 (pl. 427, figs. 3a, b).

Figure 105. Sowerby in Gray's (1839, pl. 36, fig. 12) illustration of *Fusus buccineus*. The specimen depicted is *Xymenopsis muriciformis*.

Chile; USNM 126899, Tierra del Fuego, Intertidal; USNM 348720, Puerto Harberton, Tierra del Fuego; USNM 368273, Port Williams, Malvinas (Falkland) Is., in 18 m; USNM 368401, Port Stanley, Malvinas (Falkland) Is.; USNM 368639, Punta Arenas, Chile; USNM 368641, Punta Arenas, Chile, intertidal; USNM 368654, Punta Arenas, Chile; USNM 368761, Punta Arenas, Intertidal, Chile; USNM 381693, Bahía San Sebastián, Tierra del Fuego; USNM 710029, Puerto Deseado, Santa Cruz, Intertidal; USNM 870002, 53°50'54"S, 70°30'42"W, in 15–17 m; USNM 870165, 54°05'S, 58°52'W, in 119 m; USNM 886188, 53°51'32"S, 70°25'52"W, in 2–3 m; USNM 886190, 53°51'32"S, 70°25'52"W, in 2–3 m; USNM 886737, 53°39'S, 70°55'30"W, in 20 m; USNM 886745, 53°39'S, 70°55'30"W, in 15–18 m; USNM 901628, 53°39'S,

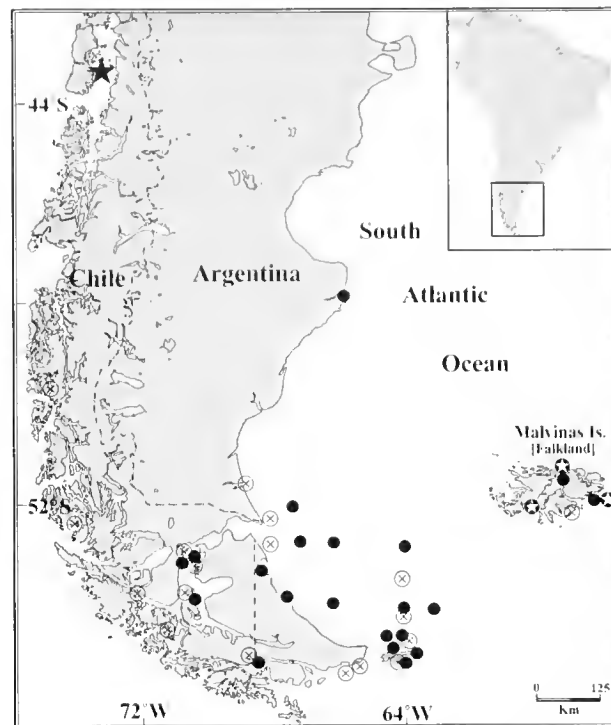


Figure 106. Localities at which *Xymenopsis* species (⊗ = *X. muriciformis*; ⊕ = *X. corrugatus*; ● = *X. buccineus*; ★ = *X. subnodosus*) were collected off Chile and Argentina.

70°55'30"W, in 20 m; USNM 901629, Strait of Magellan, 53°39.4'S, 70°55.5'W, in 24 m; USNM 901630, 53°39.4'S, 70°55.0'W, in 82 m; USNM 901631, 54°47.25'S, 64°18.3'W, in 35 m; USNM 901632, 53°33.9'S, 69°58.8'W, in 82–91 m; USNM 901633, 53°39.3'S, 70°55.4'W, 38–42 m; USNM 901634, 53°17'S, 68°13'W, in 0–1 m; USNM 901635, 53°39.8'S, 70°54.9'W, in 27–73 m; LACM 69170, Islas Guarello, Chile, 52°40'S, 73°41'W; LACM 10503, Molynieux Sound, Strait of Magellan, Chile; LACM 118051, Lively Island, East Malvinas (Falkland) Is., 52°00'S, 58°28'W; LACM 71-262, R/V HERO Cruise 712, Sta. 672, W of Puerto Año Nuevo, Isla de los Estados, Tierra del Fuego, Argentina, 54°45.1'S, 64°07.3'W, in 50 m; LACM 71-305, R/V HERO Cruise 715, Sta. 690, 8 miles E Ensenada Patagones, SE Tierra del Fuego, Argentina, 54°52'S, 65°05'W, in 144 m; LACM 71-337, R/V HERO Cruise 715, Sta. 888, W of Bahía York, Isla de los Estados, Tierra del Fuego, Argentina, 54°49.5'S, 64°19.6'W, in 56–63 m; LACM 73-66, R/V HERO, Cabo Colnett, Isla de los Estados, Tierra del Fuego, Argentina, 54°43'27"S, 64°14'18"W, in 15 m; LACM 73-68, R/V HERO, Beagle Canal, Caleta Awaikirih, Chile, 55°0'S, 69°02.2'W, in 17 m; LACM 73-69, R/V HERO, Punta Valparaíso, Canal Cockburn, Chile, 54°22.2'S, 71°21.7'W, in 15 m; LACM 73-70, Isla Carlos III, Strait of Magellan, Chile, 53°39.4'S, 72°14.8'W, in 11–12 m; LACM 73-71, Punta Dashwood, Canal Smyth, southern Chile, 52°24'S, 73°39.7'W, in 12 m; LACM 73-72, Bahía Tom, Chile,

50°11.3'S, 74°47.9'W, in 14 m; LACM 73-107, R/V HERO, Collingwood, Chile, 51°52'S, 73°43.6'W, intertidal to shallow subtidal; LACM 75-49, Puerto el Hambre, Brunswick Peninsula, Strait of Magellan, Chile, 53°37'S, 70°56'W, intertidal; LACM 78-84, R/V HERO Sta. B 4-6, N of Cabo Buen Tiempo, Río Gallegos, Santa Cruz Prov., Argentina, 51°16'-20'S, 68°50'-54'W, in 30 m, mud bottom; LACM 86-268.5, Canal Oeste, S side Isla madre de Dios, Ultima Esperanza, Magallanes Prov. Chile, 50°27.7'S, 75°11.5'W, in 30 m.

Literature records: R/V DISCOVERY: Sta. 52, 7.4 cables N, 17°E of Navy Point, Port William, East Malvinas (Falkland) Islands, in 17 m; Sta. 1230, 6.7 miles N, 62°W of Dungenes Light, Strait of Magellan, in 27 m; Sta. WS784, N of Malvinas (Falkland) Islands, 49°47.75'S, 61°05'W, in 170 m (Powell, 1951); Sta. 24.25, Puerto Edén in 10-12, 6-7 m respectively; 30.33 Puerto Edén, in 8-10 and 11-12 m; Sta. Caleta Lackawana in 4-6 m; Sta. 43 Paso Indio; Sta. 50, 63, 65 Puerto Williams, Navarino Is. (Dell, 1971).

Distribution (figure 106): Known from 45° S (Chonos Archipelago), Southern Chile (*vide* Dell, 1971 as *X. decolor*); Tierra del Fuego, Strait of Magellan, Beagle Channel (Argentina) and the Malvinas (Falkland) Islands. The bathymetric range for *X. muriciformis* is 0-170 m.

Remarks: *Xymenopsis muriciformis* has a long and complicated taxonomic history. The oldest name to have been applied to the *Xymenopsis* characterized by spiral sculpture that appears as incised grooves is *Buccinum muriciforme* King and Broderip, 1832. There were 2 lots of syntypes, BMNH 1837.12.15.2695 (2 specimens) and BMNH 1992056 (5 specimens), both from Strait of Magellan. One specimen BMNH 1837.12.15.2695 (figures 14-16), was illustrated by Dell (1972:8, figs. 31,32) as the holotype (an inadvertent lectotype designation). The holotype of *Fusus decolor* Philippi, 1845 (figures 9-10), also from the Strait of Magellan, clearly represents a worn specimen of *X. muriciformis*. The next name to be applied to this species is *Buccinum cancellarioides* Reeve, 1847, based on 2 syntypes lacking locality data. One specimen is here designated as lectotype (figures 17-19). Powell (1951) recognized *B. cancellarioides* to be an earlier name for *Fusus liratus* Gould, 1849 (Holotype, figures 1-3). Because he was unsure if Reeve's (February, 1847) name was a junior homonym of *Buccinum cancellarioides* Basterot in Grateloup, given as 1847 by Sherborn (1924:1030), he retained the use of *X. liratus*. The holotype of *Trophon loebbeckei* Kobelt, 1875 (figures 4-6), from an unknown locality, also matches closely the holotype of *B. muriciforme*, as do the lectotypes of *Trophon lebruni* and *Trophon violaceus*, both Mabille and Rochebrune in Rochebrune and Mabille, 1889. *Trophon lebruni* was based on 3 syntypes, MNHN unnumbered, all from Santa Cruz, Argentina. One specimen is here designated as the lectotype (figure 13). The figured syntype of *Trophon violaceus* MNHN

unnumbered, from Baie Orange, Tierra del Fuego is here designated lectotype (figures 7-8).

In his publication on the molluscan fauna of the Magellanic Province, Strebel (1904) proposed numerous taxa based on minor phenotypic variants. Among these were 16 species and varieties of *Trophon* that were subsequently referred to *Xymenopsis* by Powell (1951). According to Dance (1986:227), Strebel's collections were housed in the Hamburg Museum and "totally destroyed" during World War II. However, this appears to be true only for the "dry" (shell only) specimens. The alcohol preserved material on which much of Strebel's (1904) Magellanic publication was based, survived the war and is in the collections of the Zoologisches Institut und Zoologisches Museum der Universität Hamburg. Material collected by the Swedish Sudpolar-Expedition, including types of taxa described by Strebel (1908), is in the Swedish Museum of Natural History in Stockholm.

The senior author visited both these museums in the course of this study, and was able to locate much of Strebel's type material. Examination of the types of: *Trophon paessleri*, *T. elongatus*, *T. pseudoelongatus*, *T. albus*, *T. acuminatus*, *T. couthouyi*, *T. elegans* and *T. obesus* leaves no doubt that these are, at most, minor morphological variants of *Xymenopsis muriciformis*. The taxon *Trophon paessleri* is based on 6 syntypes, ZMH unnumbered, 5 from Port Grappler, Smyth Channel, Strait of Magellan and 1 from Punta Arenas. One specimen (figures 26-28) from Port Grappler is here designated as lectotype. The type material of *Trophon elongatus* consists of 7 syntypes, ZMH unnumbered, 2 from Puerto Angosto, Strait of Magellan, 3 from Puerto Bueno, 1 from Navarino Is. and 1 from Eden Harbor. One specimen (figures 35-37) from Puerto Angosto is here designated as lectotype. *Trophon couthouyi* is based on 3 syntypes, ZMH unnumbered, from Port Grappler, Smyth Channel. One specimen (figures 23-25) is here designated as lectotype. Holotypes are illustrated for *Trophon pseudoelongatus* (figures 29-31), ZMH unnumbered, and *T. albus* (figures 38-40), ZMH unnumbered, both from Ushuaia; and *T. acuminatus* (figures 20-22), ZMH unnumbered, from Punta Arenas, Strait of Magellan. *Trophon elegans* is based on 3 specimens from Port Stanley, Malvinas (Falkland) Is. One specimen (figures 11-12) ZMH unnumbered, is here designated as lectotype. *Trophon obesus* is represented by 2 syntypes from Punta Arenas, Chile; one (figures 32-34), ZMH unnumbered, is here designated as lectotype.

The type material of *Trophon paessleri* var. *turrita* and of *T. fenestratus* could not be found, and was among the material destroyed during World War II (Hausdorf *in litt.*). Based on Strebel's (1904) descriptions and figures, there is no doubt that both these taxa are conspecific with *Xymenopsis muriciformis*. We therefore designate the lectotype of *Buccinum muriciforme* (BMNH 1837.12.15.2695) as the neotype for both *Trophon paessleri* var. *turrita* and *T. fenestratus*, making both these taxa objective junior synonyms of *Buccinum muriciforme*.

Xymenopsis corrugatus (Reeve, 1848)
(Figures 57–71, 80–82, 106)

Fusus corrugatus Reeve, 1848: pl. 20 figs. 84 a, b; Kobelt, 1878: 293, pl. 74, figs. 15–16.

Trophon corrugatus Reeve—Tryon, 1880: 145, pl. 33, fig. 352; Rochebrune and Mabille, 1889: 11 54.

Trophon muriciformis Sowerby, 1880: 66, pl. 3, fig. 41. [not *Buccinum muriciforme* King and Broderip, 1832]

Trophon hoylei Strebel, 1904: 227, pl. 8, figs. 68 a–f, 69 a–c; Melvill and Standen, 1907: 137.

Trophon brucei Strebel, 1904: 230, pl. 8, fig. 72; Melvill and Standen, 1907: 135.

Trophon ornatus Strebel, 1904: 231, pl. 8, fig. 73.

Trophon standeni Strebel, 1904: 232, pl. 7, fig. 67.

Trophon A—Strebel, 1904: 234, Pl. 8, fig. 78.

Trophon B—Strebel, 1904: 235, Pl. 8, fig. 79.

Trophon falklandicus Strebel, 1908: 39, Pl. 1, figs. 5a–c.

Xymenopsis falklandicus Strebel—Powell, 1951: 159, Pl. 9, figs. 46, 47; Castellanos and Landoni, 1993: 18, pl. 3, figs. 37, A.

Xymenopsis corrugatus (Reeve)—Cernohorsky, 1977: 118, fig. 19.

Diagnosis: Axial sculpture of regular, thin, slender, rounded ribs, 19–24 on body whorl. Spiral sculpture of rounded cords (4–6 on penultimate whorl, 19–26 on body whorl), slightly broader to slightly narrower than intervening spaces, producing weakly cancellate surface at intersection with axial ribs. Spiral threads present between adjacent cords. Outer lip without apertural teeth.

Description: Shell of medium size (25–32 mm), thin, fusiform. Protoconch worn on all specimens, but clearly multispiral, conical. Teleoconch of up to 6 rounded whorls. Spire high, $< \frac{1}{2}$ shell length. Spire angle $\approx 45^\circ$. Suture deeply impressed; subsutural ramp small, but present. Aperture semicircular; outer lip rounded, distinctly crenulated, reflecting spiral cords at lip edge; inner lip curved, adpressed; interior glossy brownish. Siphonal canal short, oblique, open. Umbilicus absent. Axial sculpture of regular, thin, slender, rounded ribs, 19–24 on body whorl. Growth lines present throughout shell, clearly defined over the nodes. Spiral sculpture of rounded cords (4–6 on penultimate whorl, 19–26 on body whorl), slightly broader to slightly narrower than intervening spaces, producing weakly cancellate surface at intersection with axial ribs. Finer spiral threads present between adjacent cords. Shell ultrastructure as in *X. muriciformis*, composed of 2 layers: outer layer (0.55 shell thickness) of amorphous calcite, with ribs, cords confined to this layer; inner layer (0.45 shell thickness), crossed-lamellar aragonite with crystal planes oriented perpendicular to growing edge, of relatively constant thickness. Operculum, gross anatomy, as in *X. muriciformis*. Radula (figures 75–76) very similar to that of *X. muriciformis*. Rachidian teeth narrower ($< 100 \mu\text{m}$), in proportion to smaller size of this species. Central, lateral cusps more conical, less cylindrical than in *X. muriciformis*, inner lateral denticles of *X. corrugatus* proportionally larger.

Type material: [*Fusus corrugatus*] Holotype (figures

57–59), BMNH 74.12.11.153, lacks locality data; [*Trophon hoylei*] Lectotype (figure 60–62), ZMH unnumbered, here designated, with 4 paralectotypes, all from Port Stanley, Islas Malvinas (Falkland); [*Trophon brucei*] Type material could not be located at ZMH. No locality explicitly associated with this species by Strebel. The holotype of *Fusus corrugatus* (BMNH 74.12.11.153) is here designated as neotype of *Trophon brucei*; [*Trophon ornatus*] Holotype (figures 69–71) ZMH unnumbered, from Port Stanley, Malvinas (Falkland) Is.; [*Trophon standeni*] Original type material, from Malvinas (Falkland) Is., could not be located at ZMH. The holotype of *Fusus corrugatus* (BMNH 74.12.11.153) is here designated as neotype of *Trophon standeni*; [*Trophon falklandicus*] Holotype (figures 63–65), NIHM 1049, Berkeley Sound, Malvinas (Falkland) Is., ($51^\circ 35'S$, $57^\circ 56'W$), in 25–30 m, Station 49.

Additional material examined: MACN 10136, Malvinas (Falkland) Is., in 0 m; USNM 173062, Malvinas (Falkland) Is.; USNM 368288, Port Stanley; USNM 368292, Port Stanley, shore; USNM 368311, between Pembroke Is and Tussock Is. Malvinas (Falkland) Is., in 27 m; USNM 368342, Port Stanley, shore; USNM 368347, Port Stanley, shore; USNM 368350, Port Stanley, Malvinas (Falkland) Is.; USNM 368360, Port Stanley, shore; USNM 368389, Port Stanley, shore; USNM 368422, Port Stanley, shore; USNM 368432, Port Stanley; USNM 421877, Port Stanley; USNM 421884, Port Williams, York Bay, Malvinas (Falkland) Is.; USNM 421890, Port Stanley; USNM 655342, Port Stanley area; USNM 702124, Port William, in 16 m; LACM 15394, LACM 15395, LACM 55989, LACM 61583, all from Fox Bay, East Malvinas (Falkland) Is.

Literature records: [as *X. falklandicus*] R/V DISCOVERY: Sta. 55, 2 cables S, $24^\circ E$ of Navy Point, Entrance to Port Stanley, East Falkland Island, in 10–16 m; Sta. 56, 1.5 cables N, $50^\circ E$ of Sparrow Point, Sparrow Cove, Port William, East Falkland Island, in 10.5–16 m (Powell, 1951).

Distribution: All specimens belonging to this species that we were able to examine were from the Malvinas (Falkland) Islands. The bathymetric range of *X. corrugatus* is 0–27 m.

Remarks: The holotype of *Fusus corrugatus* BMNH 1874.12.11.153, was illustrated by Cernohorsky (1977, fig. 19). *Trophon ornatus* is based on 1 specimen (figures 69–71) ZMH unnumbered, from Port Stanley, Malvinas (Falkland) Is. The type material of *Trophon brucei*, and *T. standeni* could not be found at ZMH. In the original description, Strebel wrote that this material was sent to him from Manchester Museum by Bruce. According to D. Penney (*in litt.*), these specimens never reached Manchester again. We therefore consider the type material of both species to be lost. These taxa are considered synonyms of *Xymenopsis corrugatus* based on Strebel's (1904) descriptions and figures. The holotype of *Fusus corrugatus* (BMNH 1874.12.11.153) is here des-

ignated as the neotype for both *Trophon brucei*, and *T. standeni* making both these taxa objective junior synonyms of *Fusus corrugatus*.

Xymenopsis buccineus (Lamarck, 1816)
(Figures 52–56, 75–79, 104, 106)

- Fusus buccineus* Lamarck, 1816: pl. 427, figs. 3a, b, Liste: 6.
Fusus albidus Philippi, 1846: 119 pl. 3, fig. 5.
Fusus textilosus Hombron and Jacquinot in Rousseau, 1854: 108, Pl. 25, fig. 9–10, non Deshayes, 1835.
Fusus textilosus Hombron and Jacquinot [error for *F. textilosus*]. Hupé in Gay, 1854: 162; Philippi, 1855: 206.
Fusus Jacquinoti Philippi, 1855: 206, new name for *F. textilosus* Hombron and Jacquinot, 1854, not *F. textilosus* Deshayes, 1835.
Trophon albidus Philippi—Kobelt, 1878: 293, pl. 74, figs. 11–12; Strebel, 1904: 222, pl. 7, figs. 64 a–d.
Trophon muriciformis Sowerby, 1850: 66, pl. 3, fig. 40. [not *Buccinum muriciforme* King and Broderip, 1832]
Trophon buccineus Gray—Tryon, 1880: 146, pl. 39, fig. 490.
Trophon textilosus (Hombron and Jacquinot)—Rochebrune and Mabille, 1889: H.55.
Trophon ringei Strebel, 1904: 242, pl. 8, fig. 77.
Xymenopsis albidus (Philippi)—Powell, 1951: 159, fig. M. 90; Vokes, 1991: 7, fig. unnumbered; Castellanos and Landoni, 1993: 17, pl. 3, figs. 38B, 41–42.

Diagnosis: Axial sculpture of irregular, very weak ribs (25–28 on body whorl). Irregular, obsolete growth lines present throughout shell. Spiral sculpture of flattish cords (9 on penultimate whorl, 17–20 on body whorl) as broad as intervening spaces, forming weakly cancellate sculpture at intersections with axial ribs. No spiral threads between adjacent cords.

Description: Shell of medium size (≤ 30 mm), thin, fusiform, dirty white to brownish tan. Protoconch tall, conic, of 3 whorls. Teleoconch of up to 6 convex whorls, spire high, $\approx \frac{1}{4}$ shell length. Suture deeply impressed. Aperture subovate; outer lip evenly rounded, weakly crenulated; inner lip gently concave; interior glossy, whitish. Siphonal canal long, narrow for genus, oblique, open. Umbilicus absent, pseudoumbilical chink in some specimens. Axial sculpture of irregular, very weak ribs (25–28 on body whorl). Irregular, obsolete growth lines present throughout shell. Spiral sculpture of flattish cords (9 on penultimate whorl, 17–20 on body whorl) as broad as intervening spaces, forming weakly cancellate sculpture at intersections with axial ribs. Shell ultrastructure of two layers, as in other *Xymenopsis*, but outer, calcitic layer thinner (0.35 shell thickness), than inner aragonitic layer (0.65 shell thickness). Operculum, gross anatomy, as in *X. muriciformis*. Radula (figures 75–76) more similar to that of *X. corrugatus* than to *X. muriciformis* in that lateral cusps broader, more triangular in outline, inner lateral denticles more pronounced. Weak outer lateral denticles present in some individuals of *X. buccineus* (figure 75, arrow).

Type material: [*Fusus buccineus*] Lost, not in Paris or Geneva (Bouchet *in litt.* and Finet *in litt.*), type lo-

cality unspecified. Neotype, (figures 52–54), USNM 870410, here designated, 53°32'S, 64°57'W, in 119–124 m; [*Fusus albidus*] Probably lost, not in MNHNS, type locality unspecified; [*Fusus textilosus* Hombron and Jacquinot, 1854, not *F. textilosus* Deshayes, 1835] Holotype (figures 55–56), MNHN no catalog number, Strait of Magellan; [*Trophon ringei*] Original type material, from Strait of Magellan, destroyed, (B. Hausdorf, *in litt.*). The Neotype of *Fusus buccineus*, USNM 870410, is here designated as the neotype of *Trophon ringei*.

Additional material examined: MACN 12553, Tierra del Fuego; MACN 23862, 51°46'S, 68°45'W, in 22 m; MACN 25012 + MACN 25013, 54°26'S, 64°53'W, in 112 m; USNM 110731, Strait of Magellan, East Entrance, in 10 m; USNM 110782, Strait of Magellan, East Entrance, in 18 m; USNM 152892, Santa Cruz, Patagonia; USNM 870481, 53°40'S, 66°20'W, in 81 m; USNM 870491, 53°42'S, 66°19'W, in 81 m; USNM 881098, 54°34'S, 63°50'W, in 118 m; USNM 881924, 54°27'S, 66°12'W, in 0 m; USNM 881961, 53°32'S, 64°57'W, in 119–124 m; USNM 881966, 52°30'S, 67°14'W, in 82 m; USNM 901625, 53°39.8'S, 70°54.9'W, in 27–73 m; USNM 901626, 53°06'S, 67°04'W, in 86 m; USNM 901627, 54°59.9'S, 64°50'W, in 438 m (dead specimens); LACM 71-302, R/V HERO Cruise 715, sta. 687, 5 miles E of San Mauricio, SE end Tierra del Fuego, Argentina, 54°45'S, 64°04.6'W, in 75 m; LACM 71-313, R/V HERO Cruise 715, sta. 853, 9 miles N of Cabo Colnett, Isla de los Estados, Tierra del Fuego, Argentina, 54°34'S, 64°20'W, in 91 m; LACM 71-320, R/V HERO Cruise 715, sta. 865, 4 miles E of Isla Observatorio, Isla de los Estados, Tierra del Fuego, Argentina, 54°39'S, 64°00'W, in 75 m; LACM 71-324, R/V HERO Cruise 715, sta. 870, 6 miles NE of Isla Observatorio, Isla de los Estados, Tierra del Fuego, Argentina, 54°34'S, 64°00.3'W, in 84 m; LACM 71-327, R/V HERO Cruise 715, sta. 873, 9 miles N of Cabo San Juan E end of Isla de los Estados, Tierra del Fuego, Argentina, 54°34'S, 63°50'W, in 118 m; LACM 71-329, R/V HERO Cruise 715, sta. 875, 5 miles S of Punta Ventana, S side of Isla de los Estados, Tierra del Fuego, Argentina, 54°54.5'S, 63°56'W, in 771–903 m (dead specimens); LACM 71-330, R/V HERO Cruise 715, sta. 876, 14 miles N of Cabo San Juan, Isla de los Estados, Tierra del Fuego, Argentina, 54°29'S, 63°50'W, in 112 m; LACM 71-333, R/V HERO Cruise 715, sta. 881, Puerto Vancouver, Isla de los Estados, Tierra del Fuego, Argentina, 54°39'S, 64°00'W, grab; LACM 71-341, R/V HERO Cruise 715, sta. 894, 5 miles SE of Cabo Kempe, Isla de los Estados, Tierra del Fuego, Argentina, 54°54.9'S, 64°19.5'W, in 263–285 m (dead specimens); LACM 71-348, R/V HERO Cruise 715, sta. 903, 13 miles N of Bahía Crossley, Isla de los Estados, Tierra del Fuego, Argentina, 54°34.3'S, 64°40'W, in 84–85 m; LACM 71-349, R/V HERO Cruise 715, sta. 904, 8 miles N of Bahía Crossley, Isla de los Estados, Tierra del Fuego, Argentina, 54°39.0'S, 64°40'W, in 84–85 m; LACM 71-351, R/V HERO Cruise 715, sta. 906, 14 miles N of Cabo San Antonio, Isla de los Estados,

Tierra del Fuego, Argentina, 54°29'S, 64°29.2'W, in 122–124 m; LACM 71-352, R/V HERO Cruise 715, sta. 907, 9 miles N of Cabo San Antonio, Isla de los Estados, Tierra del Fuego, Argentina, 54°34'S, 64°30'W, in 73–76 m; LACM 71-353, R/V HERO Cruise 715, Sta. 908, 5 miles NNE of Cabo San Antonio, Isla de los Estados, Tierra del Fuego, Argentina, 54°38.9'S, 64°30'W, in 60 m.

Literature records: R/V DISCOVERY: Sta. WS71, 6 miles N 60° E of Cape Pembroke Light, East Falkland Island, in 82 m; Sta. WSS8, Off Staten Island (Isla de los Estados), Tierra del Fuego, 54°S, 65°W to 54°S, 64°55'W, in 118 m; Sta. WS97, Between Malvinas (Falkland) Islands and Patagonia, 49°S, 62°W to 49°01'S, 61°56'W, in 146–145 m; Sta. WS222, SE of Puerto Deseado, Patagonia, 48°23'S, 65°W, in 100 m; Sta. WS243, Off Santa Cruz, Patagonia, 51°06'S, 64°30'W, in 144–141 m; Sta. WS750, NE of Malvinas (Falkland) Islands 51°50'S, 57°15.2'W, in 135–144 m; Sta. WSS05, Between Malvinas (Falkland) Islands and Patagonia, 50°11'S, 63°27'W to 50°09.5'S, 63°31'W, in 150–148 m; Sta. WSS08, Off Santa Cruz, Patagonia, 49°40.25'S, 65°42'W, in 109–107 m; Sta. WSS29, Between Malvinas (Falkland) Islands and Patagonia, 50°51'S, 63°13.5'W, in 155 m; Sta. WSS34, Off Bahia Grande, Patagonia, 52°57.75'S, 68°08.25'W, in 27–38 m; Sta. WSS38, Between Malvinas (Falkland) Islands and Patagonia, 53°11.75'S, 65°W, in 148 m; Sta. WSS61, SE of Puerto Deseado, Patagonia, 47°40'S, 64°12'W, in 117–124 m; Sta. WSS63, Between Malvinas (Falkland) Islands and Patagonia, 49°05'S, 64°09'W, in 127–117 m; Sta. WSS65, Between Malvinas (Falkland) Islands and Patagonia, 50°03'S, 64°14'W, in 126–128 m; Sta. WSS67, Between Malvinas (Falkland) Islands and Patagonia, 51°10'S, 64°15'W, in 137–144 m; Sta. WSS69, Between Malvinas (Falkland) Islands and Patagonia, 52°15.5'S, 64°13.75'W, in 187–0 [sic] m.

Distribution: Known from Southern Chile and Argentina; Tierra del Fuego, Strait of Magellan, Beagle Channel, Malvinas (Falkland) Is. The vertical distribution of *X. buccineus* ranges between 0 and 155 m. Records from greater depths are dead shells. The bathymetric and geographic ranges of this species are nearly identical with those of *X. muriciformis*, and the two species have been collected together in some trawls. (e.g. USNM 901625 (*X. buccineus*) and USNM 901635 (*X. muriciformis*) both from 53°39.8'S, 70°54.9'W, in 27–73 m.)

Remarks: *Fusus buccineus* (Lamarck, 1816) was published without locality or detailed description. The type specimen is lost (Finet, *in lit.*, Bonchet *in lit.*). Although Sowerby (*in* Gray, 1839) labelled a figure *F. buccineus*, the specimen illustrated (figure 105) is clearly *X. muriciformis*, and bears little resemblance to Lamarck's figure of *F. buccineus* (fig. 104). Strebel (1904:237) likewise noted that *F. buccineus* of Gray [actually Sowerby *in* Gray] was a different species than *F. buccineus* Lamarck.

The specimen illustrated by Sowerby is also lost (K. Way, *in litt.*).

As *Fusus buccineus* is the oldest name to be applied to any species of *Xymenopsis*, we designate as neotype (figures 52–54) a specimen (USNM 870410) that reasonably conforms to Lamarck's (fig. 104) illustration of this species. This serves to remove any ambiguity regarding the identity of *Fusus buccineus* and thus stabilize the nomenclature of the Recent *Xymenopsis*. The type locality for *Fusus buccineus* becomes the continental shelf east of Tierra del Fuego (53°32'S, 64°57'W), in 119–124 m.

The next available name for this species is *Fusus albidus* Philippi, 1846, for which no type locality was designated. As the type specimen could not be located at MNHNS, it is included in the synonymy based on Philippi's description and figure. We have not designated a neotype for *Fusus albidus* because there remains a possibility that the type will yet be located at MNHNS. The type of *Fusus textiliosus* Hombron and Jacquinot, 1854 from the Strait of Magellan, housed in MNHN, is illustrated in figures 55–56, and undoubtedly belongs to this species. The type material of *Trophon ringei* could not be found, and was among the material destroyed during World War II (Hausdorf *in litt.*). This taxon is considered to be a synonym of *X. buccineus* based on Strebel's (1904) descriptions and figures. We therefore designate the neotype of *Fusus buccineus* (USNM 870410) to serve as the neotype of *Trophon ringei*. *Trophon ringei* thus becomes an objective synonym of *Fusus buccineus*.

Xymenopsis subnodosus (Gray, 1839)
(Figures 96–103, 106)

B[uccinum] subnodosa Gray, 1839: 118.

Fusus cancellinus Philippi, 1845: 67; 1846: 117, pl. 3, fig. 2; Hupé *in* Gay, 1854: 163.

Trophon cancellinus Philippi—Kobelt, 1878: 291, pl. 74, figs. 7, 8; Rochebrune and Mabille, 1889: H.59

Diagnosis: Axial sculpture of strong, irregular ribs (12–16 on body whorl), nearly as broad and intervening spaces. Spiral sculpture of dense, evenly rounded cords, (6 on penultimate whorl, 22–24 on body whorl), broader than intervening spaces. Spiral threads present between adjacent cords. Outer lip with apertural teeth.

Description: Shell large (to 37 mm), solid, slender, fusiform, dirty white, chalky. Protoconch unknown. Teleoconch of up to 6 gently convex whorls. Spire high, $\approx \frac{1}{2}$ shell length. Spire angle $\approx 45^\circ$. Suture strongly impressed. Aperture small, ovate; outer lip thickened, with 8–10 weak teeth; inner lip concave, thickly glazed; interior whitish. Siphonal canal long, oblique, open. Pseudumbilical chink, small but present. Axial sculpture of strong, irregular ribs (12–16 on body whorl), nearly as broad and intervening spaces. Spiral sculpture of dense, evenly rounded cords, (6 on penultimate whorl, 22–24 on body whorl), broader than intervening spaces. General morphology of animal and operculum

(figure 101) as in *X. muriciformis*. Oosphradium $< \frac{1}{2}$ ctenidium length, asymmetrical, with 45 and 32 leaflets on the external and internal side respectively. Ctenidium 2–3 times as wide as oosphradium, with 85–90 triangular leaflets. Radular ribbon small, short ($0.23 \times$ aperture length). Radula (figures 102–103) similar to those of *X. corrugatus* and *X. buccineus*, but with single weak denticle along outer edge of each lateral cusp.

Type material: [*Buccinum subnodosa*] Original type material from the Pacific Ocean lost (K. Way, *in litt.*). The holotype of *Fusus cancellinus*, MNHNS, is here designated as neotype of *Buccinum subnodosa*. [*Fusus cancellinus*] Holotype, MNHNS unnumbered, Strait of Magellan.

Additional material examined: BMNH 19990330, 43°38.9'17"S, 73°37.2'38"W, East side Traiguén Is., Estero Elefantes, Region 11, Chile, Dredged in 5–15 m on bottom of cobbles and dead venerids; sheltered bay.

Distribution: Known from the Strait of Magellan, and Traiguén Island, Chile.

Remarks: Gray (1839) introduced *Buccinum subnodosa* as a variety of *Buccinum muriciforme* (= *Xymenopsis muriciformis* King and Broderip) in a two line description without illustration. As Gray's type material is lost (K. Way, *in litt.*) this leaves some doubt as to the identity of this species. Gray's description refers to "alternate narrow low and wider convex spiral ridges" that produce tubercles as they rise over the axial ribs, features characteristic of both *X. corrugatus* and a species subsequently named *Fusus cancellinus*. Gray does not mention the prominent apertural teeth that are diagnostic of *X. cancellinus*, but it is possible that he had a subadult specimen lacking apertural teeth. Gray states that *B. subnodosa* inhabits the Pacific Ocean. *Fusus cancellinus* occurs along the Pacific Coast of Chile, while *X. corrugatus* is known only from the Malvinas (Falkland) Islands and Isla de los Estados. In order to stabilize the nomenclature of Recent *Xymenopsis*, we designate the holotype of *Fusus cancellinus* Philippi, 1845 (MNHNS) to serve as neotype of *Buccinum subnodosa* Gray, 1839. *Fusus cancellinus* thus becomes a junior objective synonym of *Buccinum subnodosa*.

We know of only two specimens of *Xymenopsis subnodosa*, including the neotype (shell only) housed at the Museum of Santiago, Chile. *Xymenopsis subnodosa* resembles both *X. muriciformis* and *X. corrugatus* in size, general shape, and in the coarseness of its axial ribs. It differs from *X. muriciformis* in having a thicker shell, narrower, more numerous, and more rounded spiral cords, and shares with *X. corrugatus* the presence of fine spiral threads interspersed between adjacent cords. *Xymenopsis subnodosa* is larger, has a higher spire, and coarser sculpture than *X. buccineus*. The most distinctive features of *X. subnodosa* are the thickening of the outer lip, and the presence of well defined apertural teeth, which occur in New Zealand members of the *Xymene* complex, but not in any other *Xymenopsis*. *Xymenopsis*

subnodosa is most similar to *X. corrugatus*, which is restricted to the Malvinas (Falkland) Islands. We provisionally retain this taxon, recognizing that it may prove to be a subspecies or rare variant of *X. corrugatus* characterized by an atavistic expression of a rare allele or alleles for apertural dentition.

SYSTEMATIC KEY TO THE GENUS *Xymenopsis*

1. Shell large, with strong, well defined axial ribs 2
 Shell small, with weak, poorly defined axial ribs 3
2. Shell thin, with spiral sculpture of flat cords much broader than intervening spaces, which appear as incised furrows *X. muriciformis*
 Shell thick, spiral sculpture of dense, evenly rounded cords, (6 on penultimate whorl, 22–24 on body whorl), broader than intervening spaces. Outer lip thickened, with 8–10 weak teeth *X. subnodosa*
3. Spiral sculpture of rounded cords slightly broader to slightly narrower than intervening spaces, producing weakly cancellate tubercles at intersection with axial ribs. Weak spiral threads present between adjacent spiral cords *X. corrugatus*
 Spiral sculpture of flattish cords as broad as intervening spaces, forming weakly cancellate sculpture at intersections with axial ribs
 *X. buccineus*

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Copulabyssia riosi, a new deep-sea limpet (Gastropoda: Pseudococculinidae) from the continental slope off Brazil with comments on the systematics of the genus

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ABSTRACT

A new bathyal species of the family Pseudococculinidae is described from samples dredged in 1987 along the continental slope of southeastern-eastern Brazil by the French research vessel *Marion-Dufresne*. The new species, allocated in the genus *Copulabyssia*, differs from the 4 other known congeners by characters of shell, external morphology, mantle cavity, and radula. Descriptions of internal morphology based on microdissections are provided, including the digestive system and the complex muscular apparatus of the odontophore. The distribution of characters of taxonomic significance at the species level in *Copulabyssia* is given in tabular format and discussed.

Key words: Mollusca, Cocculiniformia, Vetigastropoda, Lepetelloidea, bathyal, anatomy, taxonomy, odontophore.

INTRODUCTION

Bathyal samples dredged off E–SE Brazil yielded specimens of an unnamed species of the genus *Copulabyssia*, family Pseudococculinidae. Two live specimens and one empty shell were collected at three stations performed between 960–1320 m. The Pseudococculinidae and other families comprising the superfamily Lepetelloidea Dall, 1882, are included amongst the mollusks living at greatest depths in the ocean (Leal and Harasewych, 1999; Lesicki, 1998; Marshall, 1986; Wolff, 1979). The new taxon exhibits the diagnostic characters of the genus *Copulabyssia* Haszprunar, 1988. *Copulabyssia riosi* new species is herein compared with the 4 other species of the genus named to date (Lesicki, 1998): *C. corrugata* (Jeffreys, 1883) (NE Atlantic); *C. gradata* (Marshall, 1986) (SW Pacific); *C. leptalea* (Verrill, 1884) (N Atlantic); *C. similis* Hasegawa, 1997 (Japan).

MATERIALS AND METHODS

Two live-collected specimens and one empty shell were available for study. A single specimen was dissected. Mi-

crodissection was performed with the specimen immersed in 70% ethanol. The apical (distal) region of visceral mass was damaged; adjacent structures were described and are shown herein based on reconstruction. After dehydration in a standard alcoholic series, the second specimen was chemically dried for 10 min in hexamethyldisilazane (HMDS). Shells, radula, and chemically dried soft parts were coated with carbon and gold and examined and photographed under Hitachi S-570 (at National Museum of Natural History, Smithsonian Institution), Leo 440 (at MZSP), or Philips XL30 ESEM-FEG (Center for Advanced Microscopy, University of Miami) electron microscopes. Institutional abbreviations used are: MNHN, Muséum national d'Histoire naturelle, Paris, France; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; NMNH, Museum of New Zealand Te Papa Tongarewa, Wellington; NSMT, National Science Museum, Tokyo, Japan; SMNH, Natur Historika Riksmuseet, Stockholm, Sweden; USNM, National Museum of Natural History, Smithsonian Institution, Washington. Other abbreviations and text conventions are: **1, 5**, lateral teeth (lateral **5** = pluricuspid tooth); **1, 2**, marginal teeth; **ac**, anterior cartilages of odontophore; **an**, anus; **bm**, buccal mass; **br**, subradular membrane; **bs**, buccal sphincter; **df**, dorsal folds of buccal mass; **dg**, digestive gland; **ep**, epipodium; **es**, esophagus; **et**, epipodial tentacles; **gi**, gill; **go**, gonad; **gp**, genital pore; **if**, inner mantle fold; **in**, intestine; **ir**, insertion of m4 in radular sac; **is**, insertion of m5 in radular sac; **ki**, kidney; **lt**, left cephalic tentacle; **mb**, mantle edge; **mj**, jaw and peribuccal muscles; **mo**, mouth; **mp**, mesopodium; **m2**, pair of buccal mass retractors; **m3**, inner buccal mass protractors; **m4**, pair of antero-dorsal tensors; **m5**, pair of postero-dorsal tensors; **m6**, horizontal muscle; **m7**, pair of odontophore approximators; **m8**, pair of cartilage approximators; **nc**, nuchal cavity; **of**, outer mantle fold; **pa**, mantle papillae; **pc**, posterior cartilages of odontophore; **pr**, protuberance on right ten-

tacle; **re**, rectum; **ra**, radula; **rn**, radular caecum; **rs**, radular sac; **rt**, right cephalic tentacle; **sc**, subradular cartilage; **sf**, fold along gill; **sg**, seminal groove; **sm**, shell muscle; **sn**, snout; **st**, stomach; **vg**, vestigial left gill leaflet. The odontophore muscles examined in this study were also described by Haszprunar (1988: 165–167, fig. 3) for *Kurilabyssia venezuelensis* McLean, 1988. Terminology used herein (boldface) corresponds to the one used by Haszprunar as follows: **mj** = br + otr; **bs** = bs; **m2** = dr2; **m4** = rd2; **m5** = rr; **m6** = ho; **m7** = sr3 (?); **m8** = ci. The remaining small muscles described by Haszprunar (1988) could not be observed in the single specimen available for microdissection.

SYSTEMATICS

Class Gastropoda Cuvier, 1797

Subclass Orthogastropoda Ponder and Lindberg, 1996

Order Vetigastropoda Salvini-Plawén, 1980

Remarks: The superfamilies Cocculinoidea Dall, 1882, and Lepetelloidea Dall, 1882 have been united under the order Cocculiformia Haszprunar, 1987. Recent studies of gastropod phylogeny based on morphological characters (Ponder and Lindberg, 1996; 1997) suggest that Cocculinoidea is sister taxon to Neritopsina, and that Lepetelloidea is part of the order Vetigastropoda (see also Haszprunar, 1998: 664). This arrangement is followed herein. Harasewych *et al.* (1997) indicated, based on partial 18S rDNA sequences, that Cocculiformia may not constitute a clade. These latter authors, however, suggested that Cocculinoidea and Lepetelloidea are more closely related to each other and to Patellogastropoda than to Neritopsina or Vetigastropoda.

Superfamily Lepetelloidea Dall, 1882

Family Pseudococculinidae Hickman, 1983

Subfamily Caymanabyssinae Marshall, 1986

Genus *Copulabyssia* Haszprunar, 1988

Type species: *Cocculina corrugata* Jeffreys, 1883, p. 394, pl. 44, figs. 2–2a. Type locality: 59°40'N, 7°21'W, 930 m, Triton Expedition station 10.

Diagnosis: Protoconch sculpture of microscopic prismatic crystals; right cephalic tentacle exceptionally large, "swollen"; right cephalic tentacle with deep, open glandular seminal groove situated postero-dorsally; large pedal gland; gills pallial, several well-developed gill leaflets on right side, a single one on left side.

Copulabyssia riosi new species
(Figures 1–24, Table 1)

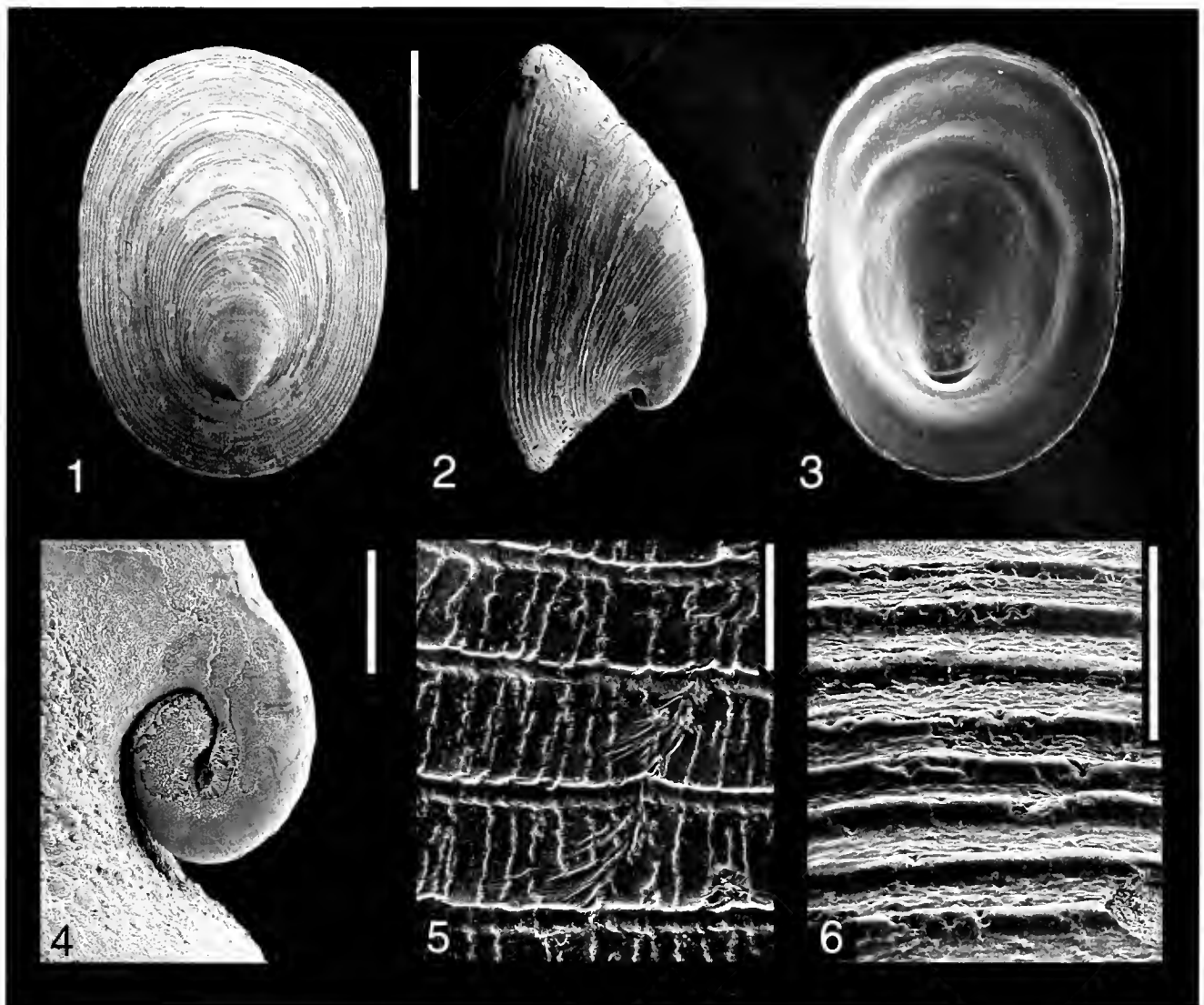
Diagnosis: Teleoconch at first with radial sculpture then with closely set concentric ribs (interspaces about 25 µm in width); internally with narrow but well-defined anterior apical septum; radial sculpture only on early teleoconch; cutting area of rachidian tooth with blunt cusp; left side of subpallial cavity with small structure

that could represent a vestigial gill leaflet; right cephalic tentacle with prominent subterminal protuberance; left cephalic tentacle small for genus; inner branches of epipodial tentacles filamentous.

Description: *Shell* (Figures 1–6): Small (length to 3.50 mm), thin, arched, elevated (height/length about 0.5), with apex at posterior quarter pointing in posterior direction. Anterior slope convex, about 88% of shell length. Posterior slope concave, about 30% of shell length. Shell surface usually lightly eroded, milky white. Protoconch (figure 4) length about 200 µm, surface badly eroded in type material. Teleoconch sculpture of concentric (commarginal) ribs separated by intervals of about 25 µm. Concentric ribs narrow (about 10 µm) and crossed by fine radial lines on early part of teleoconch (figure 5). Concentric ribs on latter part of teleoconch proportionally thicker, radial lines absent (figure 6). Internally with narrow, but well-defined, anterior apical septum. Aperture elliptical (figure 3), not conforming to a planar surface, convex. Shell muscle scar continuous, horseshoe-shaped.

Head-foot (Figures 7, 8, 13, 14, 17): Head prominent and large (about ¼ foot length) (figures 7, 13, 14, 17). Cephalic tentacles (figures 7, 13, 14, 17, rt, lt) on dorso-lateral surface of head. Right tentacle about 4 times larger than left tentacle, modified as copulatory organ (described below). Eyes apparently lacking (unpigmented?). Snout (figures 7, 13, 14, 16, 17, sn) very large, cylindrical on base, gradually becoming slightly flattened dorso-ventrally. Anterior extremity of snout almost flat, broader than region immediately behind it, with pair of small lateral projections. Foot large and flat (figures 7, 13, 14), smaller than shell aperture in preserved animal. Mesopodium (figures 7, 13, 14, mp) flattened. Epipodium (figures 7, 13, 14, ep) flange-like, surrounding entire mesopodium, larger on anterior edge, which covers baso-ventral region of snout. Pair of epipodial tentacles (figure 7, 9, 13, 14, et) well-developed, projecting from posterior region at both sides of longitudinal axis of animal, slightly dorsal to epipodium, on intersection between mantle and shell muscle. Each epipodial tentacle bifid; outer branch shorter and with broad tip; inner branch longer and pointed. Shell muscle (figures 15–17, sm) horseshoe-shaped (concavity towards anterior region); anterior extremities broader, pointing away from shell apex. Almost all head-foot muscles converge toward insertion of shell muscle.

Mantle cavity (Figures 12–15, 17): Mantle edge (figures 12–14, 17, mb) thick, with 2 folds; outer fold (figures 12, 14, 17, of) covered by slender and very small, translucent papillae (figure 12); inner fold (figures 14, 17, if) about twice as broad as outer fold, richly glandular, white. A small, transparent, yellowish protuberance (figure 13, vg) on inner margin of inner fold, in region adjacent to left cephalic tentacle, may represent vestigial left gill leaflet. Mantle cavity surrounding entire head-foot, somewhat deep, i.e., with ample space be-



Figures 1-6. *Copulabyssia riosi* new species: shell of holotype, MZSP 32150. **1.** Dorsal view. **2.** Lateral view. **3.** Ventral view. Scale line = 1.0 mm. **4.** Protoconch. Scale line = 100 μ m. **5-6.** Shell sculpture. **5.** On early teleoconch. Scale line = 50 μ m. **6.** Close to shell margin. Scale line = 100 μ m.

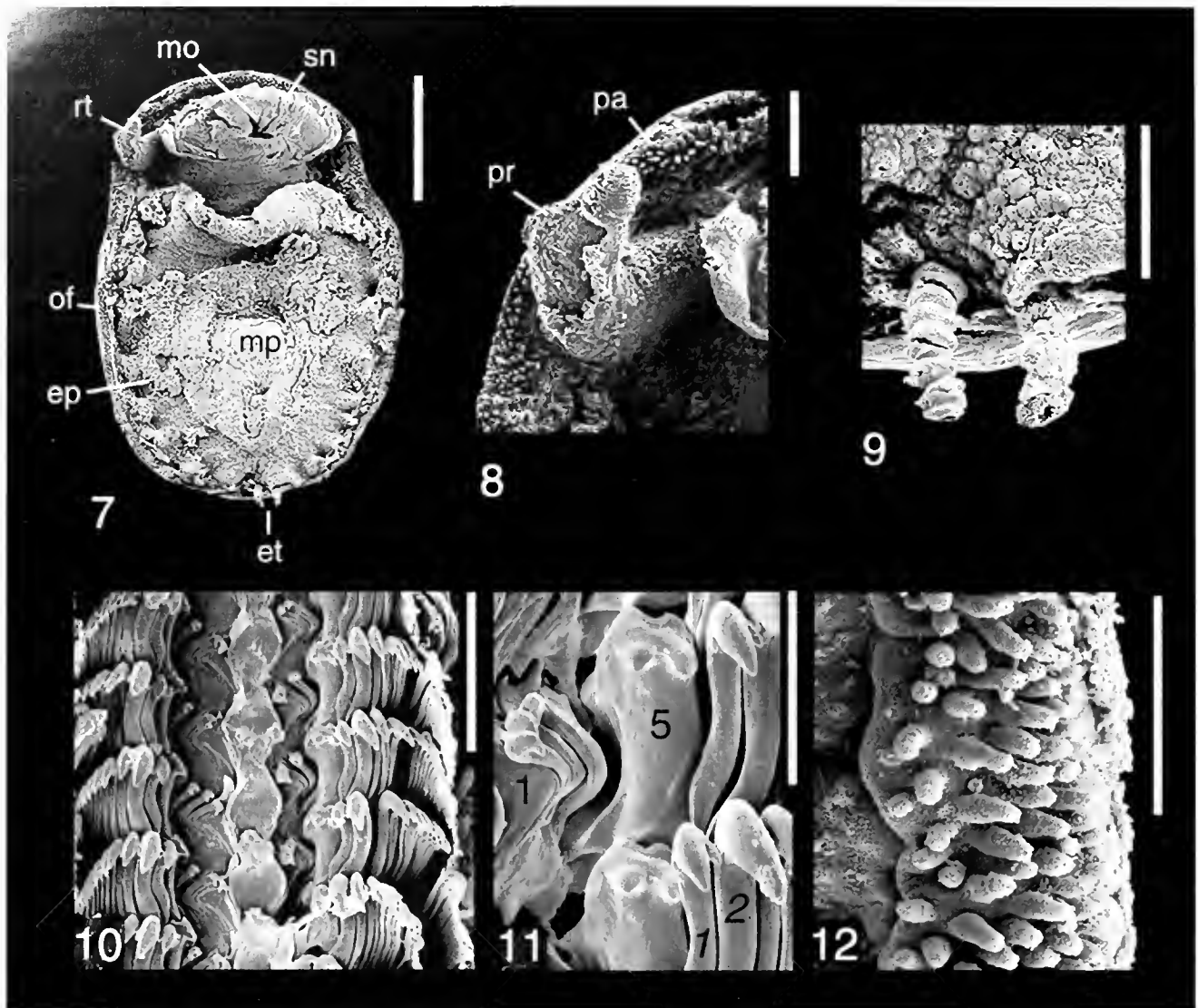
tween mantle edge and shell muscle. Nuchal cavity (figures 14, 15, 17, nc) deeper than remainder of mantle cavity. Gill (figures 13, 14, 17, gi) small, situated on right side of mantle cavity, somewhat parallel to mantle edge and extending for about half of foot length, consisting of about 14 successively smaller leaflets. Anterior extremity of gill (figure 5, gi) just posterior to head-foot limit. Each leaflet low and triangular, relatively thick. Most posterior leaflets situated perpendicularly to mantle edge, gradually becoming oblique to it on anterior region. A small, narrow, and low fold (figure 14, sf) runs between gill and shell muscle along posterior half of gill. Anus (figures 15-17, an) and genital pore (figure 17, gp) on right side, at head and foot limit, just anterior to right extremity of shell muscle.

Circulatory and excretory systems (Figures 15-17):

Heart not observed. Large blood vessels along thick mantle border. Kidney (figures 15, 17, ki) very small, white, solid, slightly triangular; situated in right-posterior region of head, just posterior to rectum.

Visceral mass (Figures 15, 16): Round, surrounded by following structures: laterally and in posterior direction by shell muscle, in anterior direction by buccal mass, ventrally by inner surface of mesopodium, and dorsally by central region of mantle and shell. Gonad (figure 15, go) and digestive gland (figure 15, dg) cream in color, intersected by several intestinal loops (figure 16). Gonad situated mainly on left region and digestive gland mainly on central region.

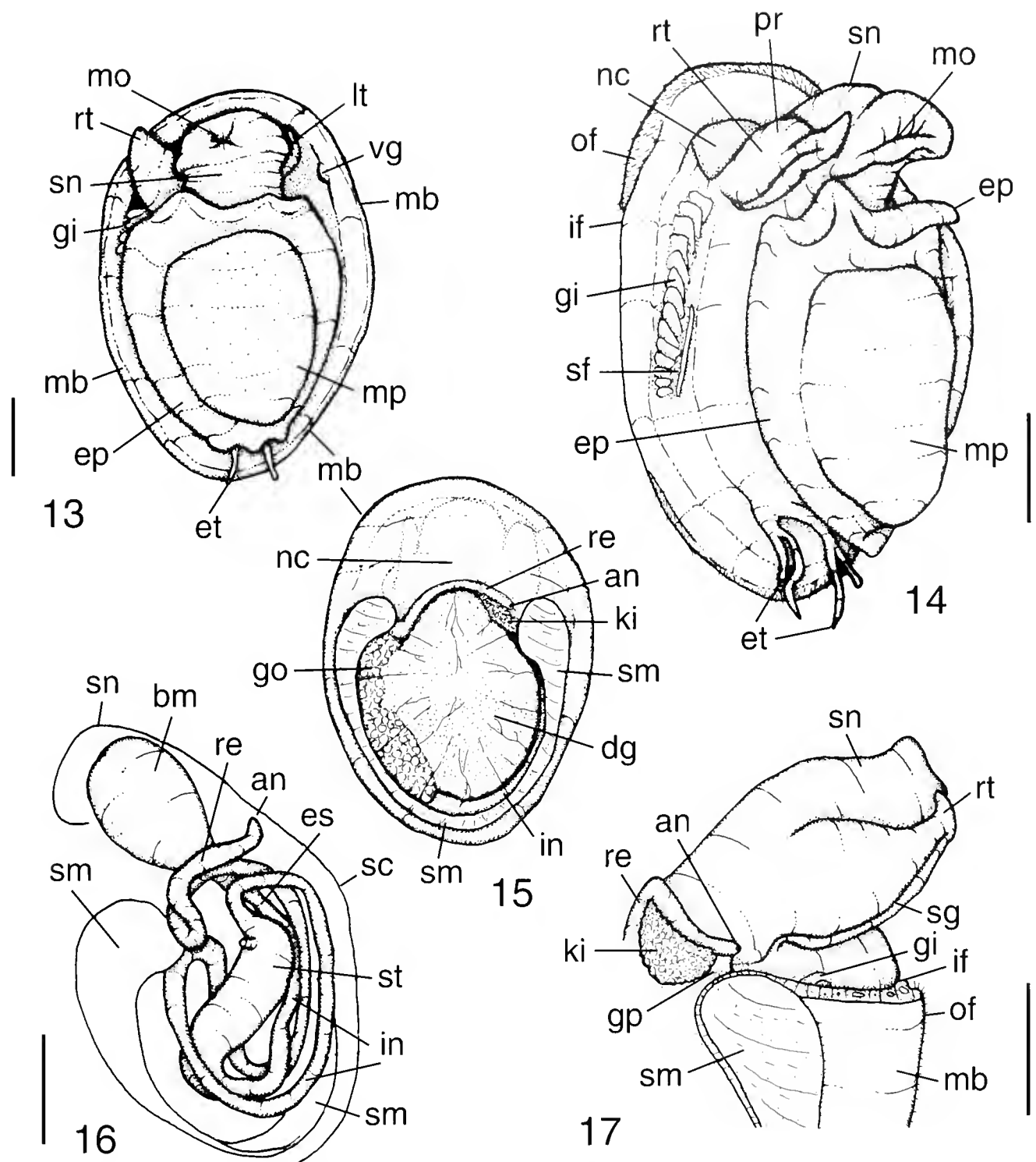
Digestive system (Figures 7, 13-24): Mouth (figures 7, 13, 14, 18, mo) on middle-ventral region of anterior sur-



Figures 7–12. *Copulabyssia riosi* new species: paratype, MNHN unnumbered, gross external morphology and radula. **7.** Ventral view of animal. Scale line = 500 μ m. **8.** Detail of right cephalic tentacle (copulatory organ). **9.** Inner branches of epipodial tentacles (damaged during preparation). Scale lines = 100 μ m. **10–11.** Radula. **10.** View of 5 rows. Scale line = 50 μ m. **11.** Detail of lateral and first marginal teeth. Scale line = 10 μ m. **12.** Papillae on outer mantle fold. Scale line = 50 μ m.

face of snout, oriented transversally. Buccal mass (figure 16, bm) somewhat large, occupying about entire head cavity. Buccal sphincter (figure 18, 19, bs) well developed. Superficial protractor muscle of buccal mass relatively narrow, connected to lateral and dorsal regions of buccal sphincter and adjacent region of snout, running along lateral and dorsal surface of buccal mass, connected to lateral and ventral region of buccal mass. Dorsal wall of buccal mass very thin, with pair of thick longitudinal folds (figure 19, df) that join together in anterior direction at median line, becoming gradually weaker toward esophagus (figures 16, 19, es). Odontophore (figures 18–24) large, comprising most of buccal mass, oval in outline. Odontophore muscles (figures 18–24): (m1) (not illustrated) several small and short fibers

connecting buccal mass to adjacent inner lining of snout, more concentrated on dorsal surface; (m2) (figures 18, 19) pair of narrow retractor muscles of buccal mass connected to inner ventral lining of snout just posterior to buccal mass, running parallel to radular sac (figures 19–23, rs), connected to postero-dorsal surface of buccal mass on lateral surface of beginning of esophagus; (m3) (figure 21, 22) pair of thin inner protractor muscles of buccal mass connected to inner lateral lining of mouth, running on (and covering) lateral surface of odontophore, connected to antero-ventral margin of posterior cartilages; (m4) (figures 20–24) pair of antero-dorsal tensor muscles connected in part to outer ventral surface of anterior cartilages and in part to lateral surface of posterior cartilages, running along (and covering) pos-



Figures 13–17. *Copulabyssia riosi* new species: paratype, MZSP 32149, gross morphology. **13.** Ventral view. **14.** Lateral view, right side, margin of mantle deflected to show its inner surface. **15.** Dorsal view. **16.** Digestive system, dorso-lateral view, left side, shown by transparency, only dorsal contour and part of shell muscle shown. **17.** Detail of head, lateral view, right side, adjacent mantle removed by means of an incision around shell muscle. Scale lines = 500 μ m.

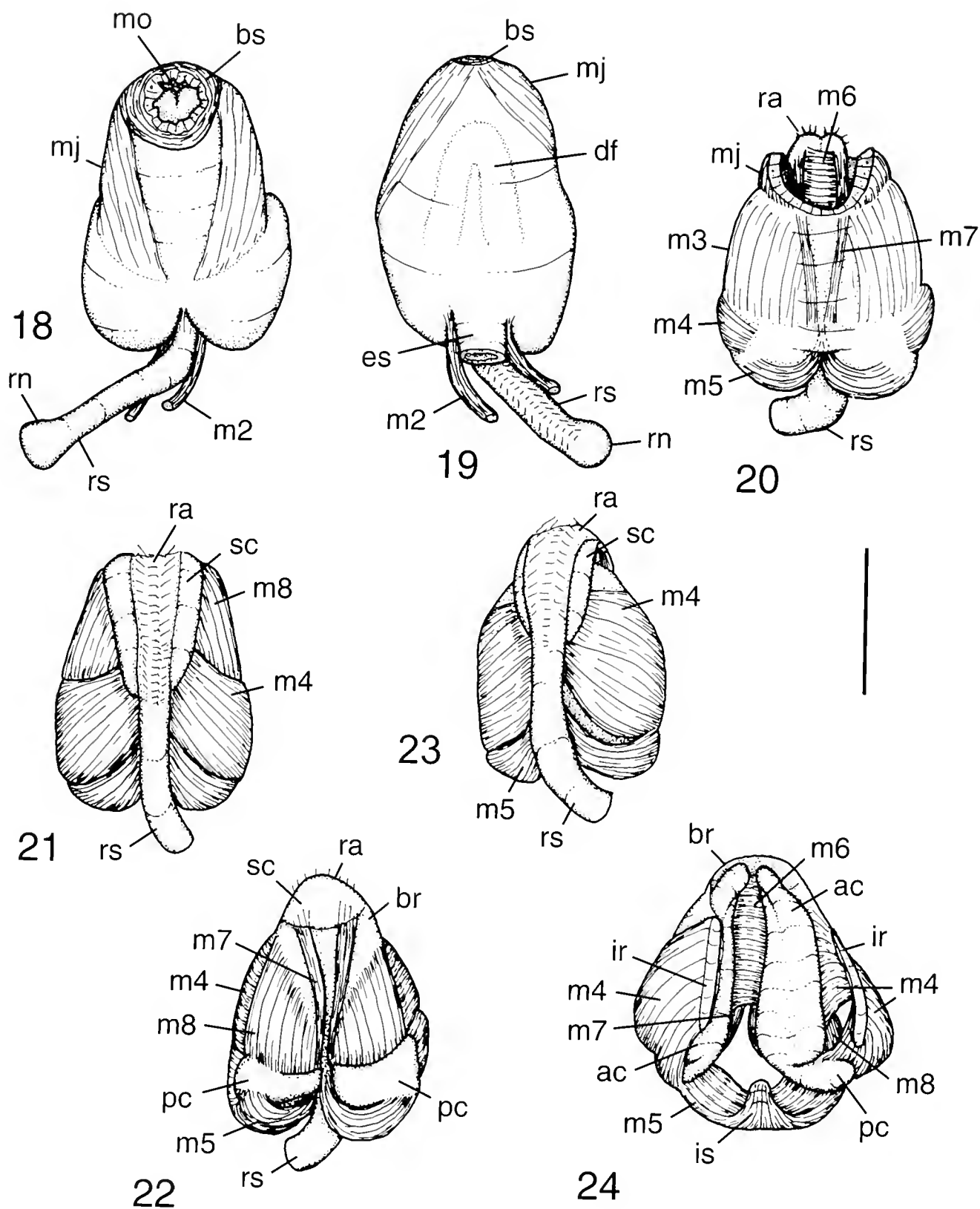


Table 1. Diagnoses of species of *Copulabyssia*. "Shell length" is maximum size for species. "Rib interspaces" is the distance between concentric ribs on posterior shell slope. "Left gill leaflet" is size of single-leaflet gill in relation to right gill leaflets; medium would be about the same size as right gill leaflets. "Right cephalic tentacle" = copulatory organ ("RT"). Unknown character states indicated by "NA". Degree of development of cephalic tentacles is relative to other congeneric species.

| Distribution | <i>C. riosi</i> Off SE, E Brazil | <i>C. leptalea</i> NW Atlantic | <i>C. gradata</i> Off New Zealand | <i>C. corrugata</i> NE Atlantic, Med | <i>C. similis</i> Japan |
|-----------------------------------|-------------------------------------|---|--------------------------------------|--|----------------------------|
| Character | | | | | |
| Shell length (mm) | 3.50 | 2.45 | 1.95 | 1.35 | 3.36 |
| Rib interspaces (μm) | ± 25 | ± 40 | ± 40 | ± 130 | ± 50 |
| Radial sculpture | early teleo only | strong | lacking | present | very weak |
| Position of apex | anterior 2/10 | anterior 3/10 | anterior 3/10 | anterior 1/10 | variable |
| Apical septum | present | absent | absent | absent | absent |
| Rachidian | broad | broad, round sides | broad | elongate | broad |
| Rachidian cutting area | blunt cusp | long, pointed cusp | cusplless, rounded | cusplless, squarish | cusplless, round |
| Cusps lateral tooth 5 | 2-3 | 4 | NA | 2 | 2 |
| Epipodial tentacles | filamentous | NA | NA | stubby | present |
| Right cephalic tentacle | well-developed | NA | swollen base | swollen base | "bilobed" |
| Left cephalic tentacle | very reduced | NA | normal | normal | normal |
| RT protuberance | well-developed | NA | absent | absent | absent |
| Left gill leaflet | ?vestigial | NA | medium | small | ?absent |
| References | this work | Warén, 1991 McLean and Hara- sewych, 1995 | Marshall, 1986 Haszprunar, 1988 | Haszprunar, 1988 Dantart and Luque, 1994 | Hasegawa, 1997 |

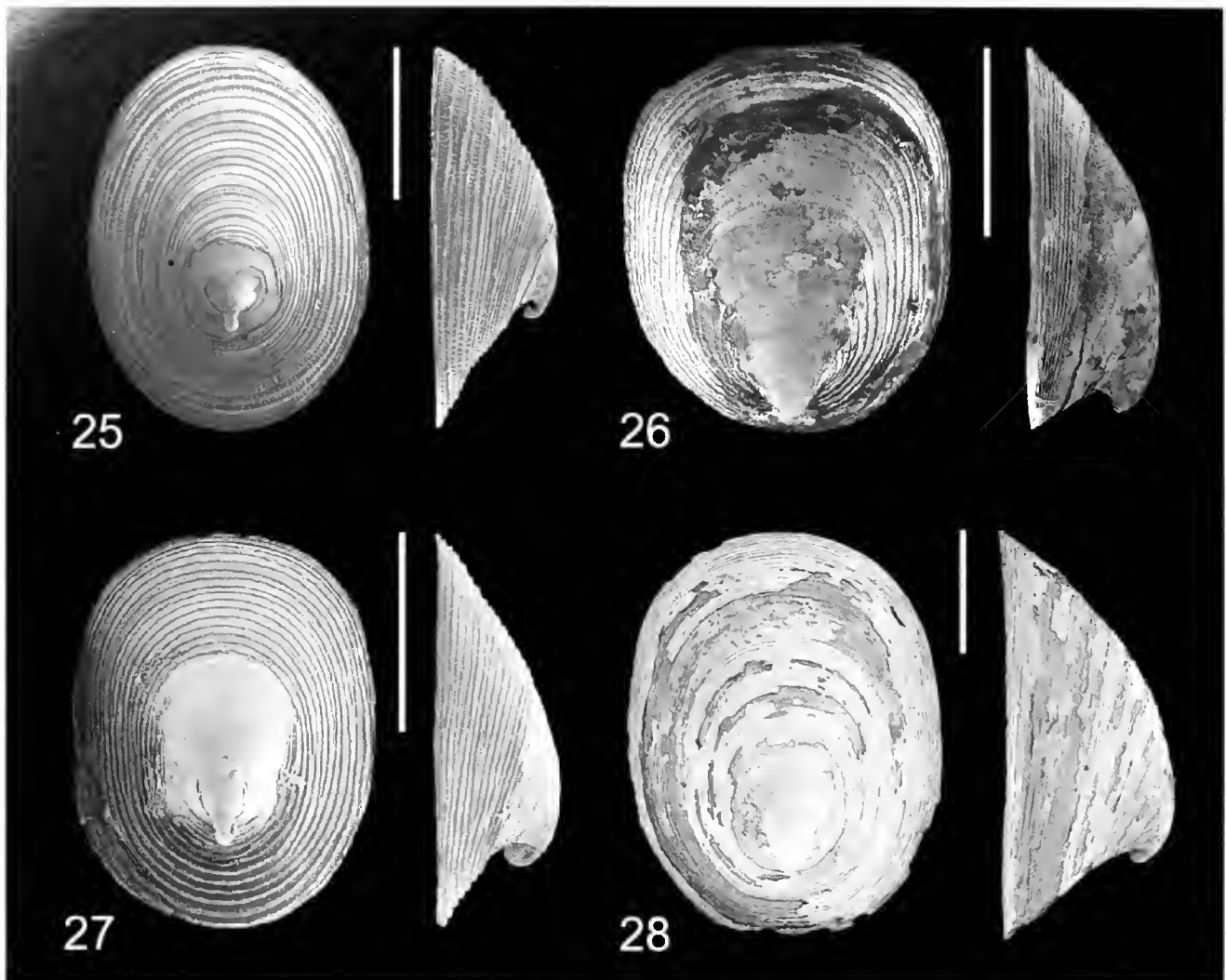
terior surface of odontophore (figure 24), connected to ventral surface of radular sac on region posterior to emergence of radula; (m5) (figures 20-24) pair of postero-dorsal tensor muscles connected to postero-ventral surface of posterior cartilages, running dorsally and medially along (and covering) posterior surface of odontophore, connected to radular sac just posterior to m4 insertion; m6) (figures 20, 24) horizontal muscle relatively narrow, connected to antero-ventral margin of anterior cartilages along about $\frac{3}{4}$ of their length; m7) (figures 20, 22, 24) pair of narrow ventral tensor muscles connected to meso-ventral margin of posterior region of anterior cartilages, running along meso-ventral surface of odontophore, connected to antero-ventral extremity of subradular cartilage (figures 21-23, sc); m8) (figures 10, 12) pair of broad approximator muscles of cartilages connected to antero-lateral surface of posterior cartilages (figures 22, 24, pc), running toward anterior cartilages, connected along lateral surface of anterior cartilages (figure 24, ac). Anterior cartilages of odontophore flattened, long, narrower in anterior direction, broader in posterior direction. Posterior cartilages short (about $\frac{1}{5}$ of anterior cartilage length), semi-spherical. Anterior and posterior cartilages joined together on small area close to median line (figure 24). Esophagus (figures, 16, 19, es) narrow and simple, running toward postero-ventral region of vis-

ceral mass, where it suddenly bends in anterior direction to its insertion in stomach (figure 16, st). Stomach large, cylindrical, directed toward shell apex; inner surface uniform, iridescent, greenish. Single duct to digestive gland situated close to shell apex. Stomach suddenly narrows giving origin to intestine (figures 16, in), which runs toward the right and then in posterior direction, surrounding dorsal margin of shell muscle, gradually turning ventrally and in anterior direction to buccal mass, where it suddenly curves in posterior direction, running along dorsal surface of mesopodium dorsally to its posterior edge, looping dorsally to the right, running ventrally back to preceding loop, near posterior region of head, where it crosses transversally from right to left dorsally to left extremity of shell muscle, suddenly turning successively in posterior, dorsal, and anterior directions; last loop represented by rectum (figures 15-17, re) crossing transversally from left to right through kidney along posterior limit of mantle cavity. Anus (figure 15-17, an) small and simple, located on posterior right side of mantle cavity.

Radula (Figures 10-11): Asymmetrical, narrow, relatively short (about twice odontophore length). Rachidian tooth rhomboid, broad for genus, broader at mid-section, and blunt (worn?) cusp. First lateral tooth trian-

←

Figures 18-24. *Copulabyssia riosi* new species: paratype, MZSP 32149, buccal mass and odontophore. **18-19.** Buccal mass extracted from snout. **18.** Ventral view. **19.** Dorsal view. **20-24.** Odontophore. **20.** Ventral view, superficial layer of muscles and membranes partially excised. **21.** Dorsal view. **22.** Ventral view, superficial layer of muscles and membranes fully excised. **23.** Dorsal view. **24.** Dorsal view, radular ribbon and radula sac extracted, most of muscles and cartilages deflected to expose inner surfaces, right-side structures more deflected than those on left side. Scale lines = 500 μm .



Figures 25–28. Dorsal and lateral views of shells of other species of *Copulabyssia*. **25.** *C. leptalea* (Verrill, 1884). USNM 757345, NE of Norfolk, Virginia, 3080–3090 m, R/V *Gillis* cruise 750S, station 36. **26.** *C. corrugata* (Jeffreys, 1883). SMNH unnumbered, SE of Reykjanes Ridge, off southern Iceland, 250–350 m, on sunken wood. **27.** *C. gradata* (Marshall, 1986). NMNZ M. 75007, holotype, off White Island, New Zealand, 1075–1100 m, on sunken wood. **28.** *C. similaris* Hazegawa, 1997. NSMT-Mo 70S22, off Tori, Suruga Bay, Japan, 430–710 m, on sunken wood. Scale lines = 1.0 mm.

gular with outer basal projection that fits into a depression on second lateral tooth, and pointed single cusp. First lateral tooth (figure 11, 1), broad, triangular. Second, third, and fourth lateral teeth strongly curved, with two short cusps. Fifth lateral (pluricuspid) tooth (figure 11, 5) massive, club-like, with 3 subterminal denticle-like cusps. Latero-marginal plate present. Inner marginal teeth pointed, with two denticle-like lateral cusps and thick shafts (e.g., figure 11, 1, 2), decreasing in size outward. Second marginal tooth largest. Outer marginal teeth with serrations.

Reproductive system (Figures 7, 8, 13, 14, 15, 17): Gonad (figure 15, go) relatively small, on posterior left region of visceral mass, surrounded by left branch of shell muscle, right surface of digestive gland, and some intestinal loops. A very narrow gonoduct on right side (not

fully examined), running in anterior direction and apically toward right side of mantle cavity, where it opens. Genital pore (figure 17, gp) turned ventrally, just posterior to anus. Seminal groove (figure 17, sg) beginning on genital pore, running on integument surface for short distance, up to posterior region of base of right tentacle. Right tentacle broad, slightly flattened dorso-ventrally, gradually tapering to flat tip (figures 7, 8, 13, 14, 17, rt). Edges of seminal groove on posterior surface of tentacle, ending on posterior region of tip. A well-developed subterminal protuberance present on anterior surface of tentacle (figure 14).

Type material: Holotype MZSP 32150, 3.25 mm length \times 2.50 mm width \times 1.60 mm height, from type locality, P. Bouchet, J. Leal, and B. M  tivier, 27 May 1987, dead shell. Paratypes: MNHN unnumbered, 3.35

mm length \times 2.35 mm width \times 1.75 mm height, MZSP 32149 (same specimen, soft parts only), E of Cabo São Tomé, off Rio de Janeiro State, Brazil, 21°24'S, 39°56'W, 1320–1360 m depth, R/V *Marion-Dufresne* cruise MD55, station CP-04, P. Bouchet, J. Leal, B. Métivier, 9 May 1987, bottom of basaltic gravel and oxidized iron pebbles; MZSP 32151, 3.50 mm length \times 2.35 mm width \times 1.90 mm height, Doce River Canyon, off Espírito Santo State, Brazil, 19°38'S, 38°43'W, 960 m depth, R/V *Marion-Dufresne* cruise MD55, station CB-95, P. Bouchet, J. Leal, B. Métivier 30 May 1987, bottom of basaltic gravel and oxidized iron pebbles (shell broken during SEM session in Miami).

Type locality: Continental slope SE off Abrolhos coral reef system, off Bahia State, Brazil, 19°00.4'S, 37°48.8'W, 950–1050 m depth, compact dark mud and shell hash bottom, (R/V *Marion-Dufresne* cruise MD55, station DC-72).

Geographic distribution: Continental slope off E–SE Brazil.

Bathymetry: 960–1320 m.

Etymology: Named after Prof. Eliézer de C. Rios, enthusiastic Brazilian author and mentor to an entire generation of malacologists.

DISCUSSION

Specimens of *Copulabyssia riosi* were found apparently removed from the actual organic substrate of the species (see Lesicki, 1998, for a listing of species-specific substrates and food preferences in the family). The new species differs morphologically from the other four species allocated in the genus *Copulabyssia* (see figures 25–28, table 1) by the presence of an apical septum on the inner shell surface, narrow sculptural interspaces, filamentous, longer epipodial tentacles, presence of a structure on the left side of subpallial cavity that could prove to be a vestigial left gill leaflet, and by the presence of an anterior, subterminal protuberance on the right cephalic tentacle. The double insertion of the m4 and the expanded insertion of the m5 are character states unique to *Copulabyssia riosi* when compared to other species of Cocculinoidea and Lepetelloidea for which these characters are known (see Haszprunar, 1987; Simone, 1996); however, the states of these characters are so far unknown for the other four species of the genus *Copulabyssia*.

The mantle organs of *Copulabyssia riosi* are typical of the genus, with nuchal cavity and gill leaflets situated in the right side of the mantle cavity. *Copulabyssia riosi* shows a satellite fold in the inner margin of the gill, and a small protuberance that could represent a vestigial gill leaflet in the left region of the mantle border. In the superfamily Lepetelloidea, similar structures are also present in the *Addisonia enodis* Simone, 1996 (Lepetelloidea, Addisoniidae). The arrangement of loops of the digestive system looks similar to that described by Has-

zprunar (1988: 167–168, fig. 4) for *Amphiplica knudseni* McLean, 1988 (Lepetelloidea: Pseudococculinidae), but differs by the reduction of salivary glands, jaw plates, and esophageal pouches.

The complex odontophore of *Copulabyssia riosi* presents a combination of apparently plesiomorphic and autapomorphic characters. The presence of 4 odontophore cartilages and their approximator muscle (m8) represents apparently plesiomorphic states present in several species of Patellogastropoda, Vetigastropoda (including Lepetelloidea), Cocculinoidea, and Neritopsina (L. R. L. Simone, personal observation). The well-developed subradular cartilage, the partial connection between the anterior and posterior odontophore cartilages and the horizontal muscle (m6) connected only in a side of the anterior cartilages seem to represent apomorphic characters (at least in relation to Patellogastropoda).

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Invasion of the exotic freshwater mussel *Limnoperna fortunei* (Dunker, 1857) (Bivalvia: Mytilidae) in South America

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ABSTRACT

We traced the invasion and investigated the distribution of the Asian bivalve *Limnoperna fortunei* (Dunker, 1857) in South America. In addition, we comment on the problems caused by this invasive species. In 1991, *L. fortunei* was introduced into la Plata Basin (currently the only American continent drainage system invaded by this species) through Río de la Plata River. By the end of 1994 and during 1995 this species dispersed throughout the Argentine coast of the Río de la Plata River and was reported from the Uruguayan coast. In 1995 and 1996, it was first discovered in the Paraná River, in Santo Tomé (Salado del Norte River), and later up in Goya. In November, 1996, *L. fortunei* was reported in Cerrito Island, where the Paraguay River joins the Paraná River. In April 1997, it was collected in Paraguay River on Asunción Harbor, Paraguay. In 1999, it was detected in Brazil (Itapuã Beach, Municipality of Viamão, Rio Grande do Sul State). These recent records document the fast and ongoing expansion of the species geographic range, as well as its prompt adaptation to the different environments of the la Plata Basin.

Key words: South America; Neotropical Region; la Plata Basin; invasive species; distribution; biofouling.

INTRODUCTION

The la Plata Basin is one of the most important hydrographic systems in South America. It has a drainage area of approximately 3×10^6 km², and comprises 4 main sub-basins (Bonetto, 1994): (1) Uruguay River, (2) Paraná-Paraguay system, (3) Río de la Plata River, and (4) the Andean tributaries (figure 1).

A diverse, native molluscan fauna occurs along the Argentine shore of the Río de la Plata estuary (Darrigran, 1994), including 27 gastropod and 21 bivalve species. Only 4 of the bivalves are strictly freshwater and infaunal species: *Anodontites tenebricosus* (Lea, 1834), *Diplodon paranensis* (Lea, 1834), *Musculium argentinum* (d'Orbigny, 1835) and *Pisidium sterkianum* Pilsbry, 1897. The only epifaunal species on the Argentine coast of Río de la Plata River is the estuarine *Mytella char-*

ruana (d'Orbigny, 1842). Until 1993, *M. charruana* was the only Mytilidae found in Río de la Plata River, in Punta Piedras, Argentina and Montevideo, Uruguay (Darrigran and Pastorino, 1995a).

In the 1970s, 2 asiatic freshwater bivalves, *Corbicula largillierti* (Philippi, 1844) and *C. fluminea* (Müller, 1774) (Corbiculidae), entered South America along the Argentine shores of Río de la Plata River (Ituarte, 1981).

In 1991 we detected, for the first time in South America, the presence of a mytilid, *Limnoperna fortunei* (Dunker, 1857), in the Río de la Plata River shore at Bagliardi Beach (Pastorino *et al.*, 1993). This is an euryhaline freshwater species, native to China and to southeastern Asia (Morton, 1977), which resembles marine mussels (Mytilidae) in its morphology and biology.

Commerce between Argentina and the countries where *L. fortunei* is supposedly native takes place mainly by sea. Following Carlton (1992) and Carlton and Geller (1993), Darrigran and Pastorino (1995a) hypothesized that *L. fortunei* and other invading organisms may have arrived in ballast water of ships coming from southeastern Asia.

Other authors have indicated that *L. fortunei* was introduced in and recorded from Hong Kong in 1966 (Morton, 1975, 1996) and Japan in 1991 (Kimura, 1994). In the Americas, *L. fortunei* is known to have invaded only Río de la Plata Basin. Morton (1973) suggested that the morpho-functional features of this species allow for rapid expansion of its distribution range, in similar fashion to the invasive abilities of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in the Northern Hemisphere. The species exhibits 2 features that may contribute to its abilities as an invader: (1) it is the only relevant mollusk in the freshwater littoral having a byssus, and (2) has no known native competitors for physical space. As a result of the high rates of invasion, as we further discuss below, *L. fortunei* causes serious biofouling of municipal drinking water and industrial water systems. As we demonstrate below, populations of *Limnoperna fortunei* are not only rapidly increasing in density in sev-

eral localities but are also quickly expanding geographically, mostly in northward direction.

Since 1991, when it was first found at Bagliardi Beach, until the end of 1993, the species was found only in mixohaline (e.g., Punta Piedras and Punta Indio) and euryhaline environments (e.g., Magdalena Beach, Atalaya Beach, Punta Blanca, La Balandra Beach). At that time, the species had not been collected farther north than the freshwater environment of Punta Lara Beach, and was apparently absent from all other countries and rivers comprising the la Plata Basin (Darrigran and Pastorino, 1993).

The objectives of this paper are to investigate the invasion of *L. fortunei* in South America, to provide an update of its distribution in the Neotropical Region, and to emphasize the importance of this invasive bivalve in biofouling processes in the la Plata Basin.

MATERIALS AND METHODS

Collections were made along the Río de la Plata River shore at low tides. In the Paraná River, samples were collected with a 319 cm² "Tamura" dredge (Marchese and Ezcurra de Drago, 1992). Periphytic populations were sampled by hand. In the mouth of Paraguay River, "macrofouling" samplers (Stupak *et al.*, 1996) were used. Environmental parameters taken into account were: temperature, pH, and conductivity. The study localities are shown in figure 1. Specimens from the Malacological Collection of La Plata Museum, Argentina (MLP) were examined. Sampling for larvae was made using a mesh of 25 µm in Uruguay River (towns of Colón and Concepción del Uruguay), at 3 stations in the Carcarañá River, and Correntoso River.

RESULTS AND DISCUSSION

Limnoperna fortunei was first found in South America in 1991 at Bagliardi Beach (Argentina) with densities of 5 individuals·m⁻² (Pastorino *et al.*, 1993). In 1992, the maximum density recorded was about 3×10⁴ individuals·m⁻². In 1993, in the same locality, the maximum density recorded was 8×10⁴ individuals·m⁻². In 1998, densities of about 15×10⁴ individuals·m⁻² were commonly recorded, values equivalent to those for mytilid densities at the seashore in Mar del Plata, Argentina (Penchaszadeh, 1973).

In 1994 and 1995, *L. fortunei* was found in the water intakes of the town of Bernal (MLP 5204) and Retiro, and on Buenos Aires Harbor (MLP 5205). Scarabino and Verde (1994) reported the species from the town of Colonia del Sacramento, Uruguay (MLP 5202). All these localities are on the Río de la Plata estuary. During 1996, the species expanded to the town of Goya (29°10'S, 59°16'W), in Corrientes Province (Di Persia and Bonetto, 1997) and nearby lotic bodies, and was collected in the middle Paraná River, near the city of Santa Fé, where the river has a very wide alluvial plain (25 km in width; Drago, 1990).

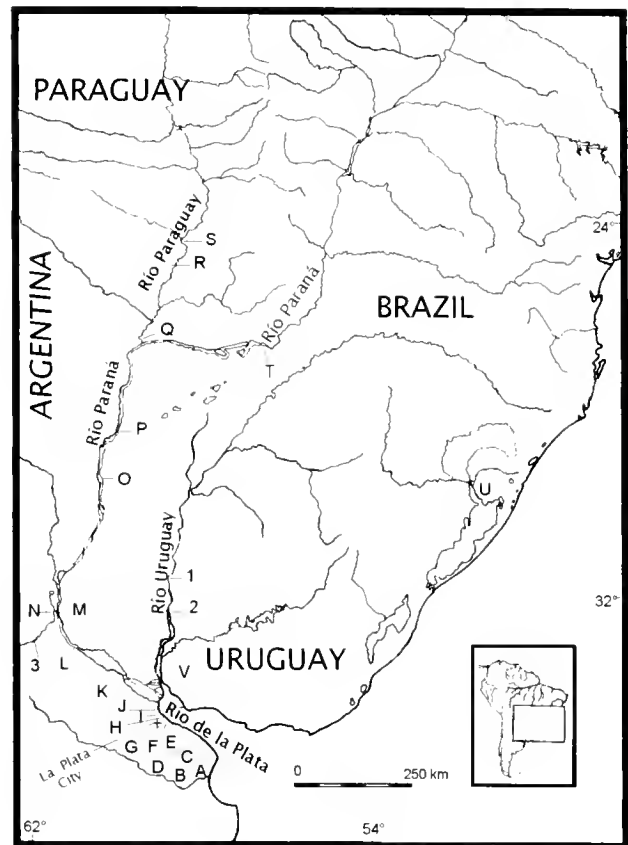


Figure 1. Studied localities on the la Plata Basin. A, Punta Piedras; B, Punta Indio; C, Magdalena beach; D, Atalaya Beach; E, Punta Blanca; F, La Balandra Beach; G, Bagliardi Beach; H, Punta Lara Beach; I, Bernal Beach; J, Buenos Aires Harbor; K, Atucha I Nuclear Power Plant; L, City of Rosario; M, Town of Santo Tomé; N, City of Santa Fé; O, Esquina; P, Goya; Q, Cerrito Island; R, Town of Formosa; S, Asunción Harbor; T, Posadas Harbor; U, Praia de Itapua (Rio Grande do Sul State, Brazil); V, Town of Colonia del Sacramento; 1, Town of Colón; 2, Town of Concepción del Uruguay; 3, Carcarañá River.

Limnoperna fortunei was first collected in Paraná River at Vuelta del Este, Zárate, on the Paraná de Las Palmas River (MLP 5206), and at Paso Burghi, city of Rosario, on the lower Paraná River (MLP 5207) toward the end of 1995 (figure 1). The species settles on all kinds of substrates across the entire floodplain. It was found in the main channel, on the left bank at town of Paraná and associated alluvial plain, in San Javier and Correntoso (MLP 5287) rivers, near the city of Santa Fé. It was also found on the right bank of the lower Salado del Norte River (MLP 5285), in the town of Santo Tomé (31°40'S, 60°45'W).

Limnoperna fortunei was part of the epifauna present on Solanaceas and *Paspalum* sp. (MLP 5286) in all habitats observed, but was not found on the sandy, moving bars (Drago, 1997) in the main channel. Perhaps due to the unfavorable sandy substrate, the central part of the

main channel provides habitat to only a few benthic species (Marchese and Ezcurra de Drago, 1992). In the Correntoso River (a secondary channel of the middle Paraná River), *L. fortunei* colonized the silty clay beds at all locations sampled.

The euryhaline attributes of *L. fortunei* probably facilitates its rapid spread. The mean salinity at the main channel of the Paraná River is 0.05 ‰, and in Correntoso River it ranges between 0.064–0.345 ‰. In Salado del Norte River, which mixes with the waters of the Paraná River, salinity varies from 0.5 to 4 ‰ (Ezcurra de Drago, personal observation). Mean pH is 7.4 in the Paraná main channel and 7.2 in secondary courses (Marchese and Ezcurra de Drago, 1992), while in Salado del Norte River pH reaches 8.7.

In 1996, this species was collected on "fouling" samplers in Cerrito Island (27°20'S, 58°43'W), near the confluence of the Paraguay and Paraná rivers (MLP 5340). In April 1997, it was collected on Asunción Harbor (25°17'21"S, 57°38'08"W), in the Paraguay River, in Paraguay (figure 1). It was also collected during the last months of 1998, at Posadas Harbor, on the upper Paraná River. In November 1999, *L. fortunei* was detected in Brazil on Itapua Beach, Municipality of Viamão, Rio Grande do Sul State (MLP 5550). No larvae, juveniles or adults have been found at any of the localities examined in Uruguay River (Colón, Concepción del Uruguay) or Carcaraña River (Carcaraña and la Ribera).

The biofouling problems caused by *L. fortunei* in South America are similar to those described for *Dreissena polymorpha*, the zebra mussel, in the Northern Hemisphere (Darrigran, 1995).

The principal problems caused by zebra mussel invasion, settlement, and maturity, into water distribution systems (Nalepa and Schloesser, 1993) are listed below (the problems which have already been detected in Argentina resulting from invasion by *L. fortunei* are marked with (X)).

- (X) Reduction of pipe diameter
- (X) Blockage of the pipeline
- Decreased water velocity caused by friction (turbulent flows).
- (X) Accumulation of empty shells
- Contamination of water pipelines by mass mortality
- (X) Filter occlusion

These problems have occurred in the intakes of water treatment plants in the city of La Plata; water treatment plants along the Corrientes River (MLP 5365), and also in industrial and power-generating plants. They cause an increase in the operational costs of these facilities due to reduced pump efficiency, increased tube corrosion (caused by proliferation of bacteria and fungi), and increased frequency of shutdowns for cleaning and filter changes.

Absence of relevant records in the numerous benthic studies conducted prior to 1991 (Darrigran, 1991, 1994; Marchese and Ezcurra de Drago, 1992) indicate that colonization by *L. fortunei* is a recent event. By late 1996

and early 1997, the first cases of fouling by *L. fortunei* in nearby industries were reported in the Paraná River (e.g., Atucha I Nuclear Power Plant and San Nicolás de los Arroyos Electric Plant (MLP 5300), Buenos Aires Province).

Based on the facts above described, it appears that the geographic range of *L. fortunei* is in continuous expansion in South America, and that the species is apparently adapting to different environments along its invasion routes. Between 1991–1999 this species invaded 4 countries (Argentina, Uruguay, Paraguay, and Brazil); 3 of the Río de la Plata Basin main rivers (la Plata, Paraná, and Paraguay). It traveled upstream at a speed of about 240 km·year⁻¹. Throughout its distribution range, *L. fortunei* inhabits a wide variety of environments: from euryhaline waters in the La Plata estuary to strictly freshwater habitats along the Paraguay and Paraná rivers.

This expansion is probably favored by the morpho-functional features of the species, and by the apparent absence of competitive interactions along the littoral of la Plata Basin. *Limnoperna fortunei* is the only relevant species using byssal epifaunal attachment among local freshwater species.

Although the distribution of *L. fortunei* is currently still limited to la Plata Basin, there are no apparent constraints that could prevent the invasion of other drainage systems. Moreover, this expansion may be favored by the increase in trade between Argentina, Uruguay, Paraguay and Brazil, as a consequence of the recently established MERCOSUR international economic consortium (Darrigran, 1995; Darrigran and Pastorino, 1995b). Additional dispersal of the species could also be favored by the international project HIDROVIA, which consists of a waterway connecting the main hydrographic systems of South America. The project comprises a complex fluvial network system that involves and interconnects Río de la Plata, Paraná, and Paraguay rivers, and includes plans for extensive basin dredging, harbor construction, and improvement of the harbors and highways. Connections among the main South American basins (e.g., Amazonas, Orinoco) are likely to be artificially established in the future. Up to now no effective control mechanisms have been proposed to prevent further spread of *L. fortunei*.

The impact of *L. fortunei* will not be restricted only to the economy, but will also affect the diversity of the native molluscan communities. Darrigran *et al.* (1998) showed that, since the introduction of *L. fortunei* at Bagliardi Beach, populations of 2 common gastropods have been displaced: *Chilina fluminea* (Maton, 1809) is no longer found, while *Gundlachia concentrica* (d'Orbigny, 1835) is becoming rare (figure 2).

In contrast, several benthic species, uncommon or absent before the occurrence of *L. fortunei*, are now present. These include Annelida Oligochaeta (8 species), Aphanoneura (1 species) and Hirudinea (8 species); plus assorted Crustacea and Insecta (Darrigran *et al.*, 1998). Additionally, we observed the epizotic colonization and smothering of native bivalves (e.g., *Anodontites trapesi-*

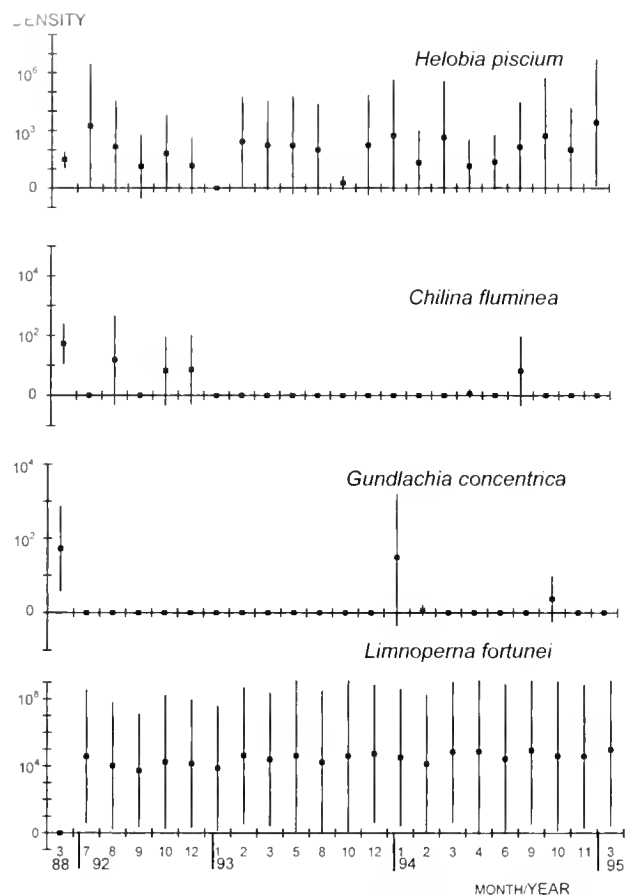


Figure 2. Temporal variation of density (individuals·m⁻², represented by mean and standard deviation) of some native mollusks associated with the byssus of *L. fortunei* in Bagliardi Beach (34°55'S, 57°49'W), Argentina.

alis (Lamarck, 1819) and *A. tenebriosus* (Lea, 1834)) by *L. fortunei*, in a behavior similar to that shown by *Dreissena polymorpha* on unionids (Parker *et al.*, 1998).

Last but not least, further expansion of the natural range of *Limnoperna fortunei* and the possibility of invasion of parts of North America by this species should not be rejected. As Ricciardi (1998) observed, "Given that shipping traffic from both Asia and South America has already resulted in recent introduction of exotic bivalves to the USA, a future North American invasion by *L. fortunei* is highly probable."

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Location of allospermatozoa in the freshwater gastropod *Biomphalaria tenagophila* (d'Orbigny, 1835) (Pulmonata: Planorbidae)

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The freshwater pulmonate *Biomphalaria tenagophila* is a simultaneous hermaphrodite. The route of allospermatozoa in the receiving partner was used in the analysis of resource allocation in the male function in this species. Allospermatozoa enter the vagina, may or may not bypass the spermatheca, continuing through nidamental gland, oviduct-muciparous gland, albumen gland, ovispermioduct, seminal vesicle, ovotestis collecting canal, and follicles of ovotestis. A new technique is proposed to label spermatozoa via injection of tritiated thymidine through the pneumostome (under anesthesia). Labeled allospermatozoa were located in the spermatheca, nidamental gland, oviduct-muciparous gland, albumen gland, seminal vesicle, and follicles of ovotestis. No relation was found between the duration of pairing and movement of the allospermatozoa through the reproductive system. It is suggested that the final destination of allospermatozoa are the follicles of ovotestis. Their presence in the spermatheca, where they may be dissolved, could be fatal. Presence of allospermatozoa in the nidamental gland, oviduct-muciparous gland, or albumen gland may be a consequence of unilateral copulation (snail plays only a receiving role), which packs the seminal vesicle with autospermatozoa. Allospermatozoa may wait in the interior of the female tract until the snail becomes a donor in a subsequent pairing. From then on, allospermatozoa may pass through an empty seminal vesicle toward their final destination, the follicles of ovotestis.

Key words: Reproduction, spermatozoa, hermaphroditic, pulmonates.

INTRODUCTION

The location of spermatozoa within the reproductive system of inseminated pulmonate gastropods plays an im-

portant role in the processes of self-fertilization, cross-fertilization and, in particular, preferential cross-fertilization in these mollusks (Larembergue, 1939; Paraense, 1959).

In the genus *Physa*, 2 or 3 possible chambers for fertilization were described. Although these chambers open in the oviduct, the actual site of fertilization may be located in the hermaphrodite region, close to the carrefour (Duncan, 1969). In planorbids, the seminal vesicle has been cited as the main location of spermatozoa (Larembergue, 1939). The fertilization chamber, in the carrefour, where the spermatozoa received from the partner are stocked, is also a possible fertilization site (Abdel-Malek, 1954; Duncan, 1975). The oviduct (Fretter and Graham, 1964) and the upper part of the ovispermioduct may be sites where the oocytes are fertilized by the allospermatozoa (Abdel-Malek, 1954). Some authors consider the spermatheca as a location where spermatozoa remain immediately after copulation, proceeding subsequently through the female ducts (Duncan, 1975). Notwithstanding, the spermatheca in *B. glabrata* also behaves as a site of lysis of spermatozoa (Horstmann, 1955; Jong-Brink, 1969; Kitajima and Paraense, 1983). In planorbids, the spermatheca is a blind, pyriform organ, opening in the vagina through a short duct (Paraense, 1975; Kitajima and Paraense, 1983). This is also called bursa copulatrix (Duncan, 1975), or seminal receptacle. In euthyneuran gastropods, the evolutionary acquisition of reproductive systems such as functional simultaneous hermaphroditism has been associated with, among other traits, fundamental changes in the structure of the spermatozoa (Thompson, 1973).

A past experiment involving incorporation of ⁵⁹Fe by *Biomphalaria glabrata* took place in water containing this radioisotope (Gazzinelli *et al.*, 1970). Incorporated isotope was transferred, during pairing, from labeled *B. glabrata* to non-labeled partners. The presence of the radioisotope in snails receiving spermatozoa was recorded chiefly in the spermatheca and collecting canal of the ovotestis (Paraense, 1976).

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Biomphalaria glabrata is known to preferentially concentrate iron in the ovotestis, as well as in non-reproductive organs such as digestive gland and mantle (Heineine *et al.*, 1969). Therefore, it is plausible that ^{59}Fe transferred from labeled to non-labeled snails could be incorporated in the ovotestis of receptor snails, independently of spermatozoa being the carrier of ^{59}Fe within the receptor snail.

On the other hand, the use of DNA-specific labels can be an efficient way of tracking the location of allospermatozoa in the inseminated snail partner. The route of spermatozoa heads in the inseminated snail can be determined by the use of tritiated thymidine (^3H Td). This method also allows for the detection of possible areas of storage and sites of cross-fertilization.

MATERIALS AND METHODS

One hundred and six specimens of *Biomphalaria tenagophila* were used both of the wild type and albino mutants. Specimens were collected in Bom Retiro, Joinville, Santa Catarina State, Brazil. They were kept for over 4 years under laboratory conditions. Each aquarium contained a tablespoon of red earth sterilized in dry incubator at 90°C for 12 h. One hundred and eighty ml filtered water, saturated with calcium carbonate, was added to each aquarium. Snails were fed daily with fresh lettuce and twice a week with a meal consisting of equal amounts of red earth, powdered whole milk, wheat germ flakes, powdered calcium carbonate, and dry powdered alfalfa. To a 5 l amount of this mixture 350 mg of vitamin E was added. Except in some cases, snails were kept in isolation from sexual immaturity onward.

Two supplies of aqueous solutions of ^3H Td were used in the experiments. Ten μl of one (USP, kindly offered by Dr. Mariano Amabis, University of São Paulo) yielded 218687 counts per min. (cpm); the other commercial solution (WM) was purchased as 1 millicurie, or 37 megabecquerel/ml; 5 μl from this solution yielded 314850 cpm in a Beckmann Liquid Scintillator 7200, using "program 2 for tritium". Each of the 106 specimens was anesthetized by immersion in a 0.05% nembutal solution for 3–4 h, depending on snail size. Afterward, they were inoculated with 5–10 μl of ^3H Td injected using microsyringe into the lung cavity, through the pneumostome. Recovery from anesthesia took place in a humid chamber, for 3–4 h, with each snail placed on its right side in a plate with water covering half shell. After this period, each inoculated snail was returned to its aquarium for completion of recovery from anesthesia and radioisotope incorporation.

Between 4–29 days after treatment, each inoculated snail (IC) was paired with a non-inoculated snail (NIC) for a period of 6–984 h. NIC snails were dissected under stereoscopic microscope within a period of 0–24 h after separation. The following organs were extracted: spermatheca, oothecal gland + muciparous gland, oviduct or oothecal gland by itself, but muciparous gland with oviduct, part of digestive gland, carrefour, albumen

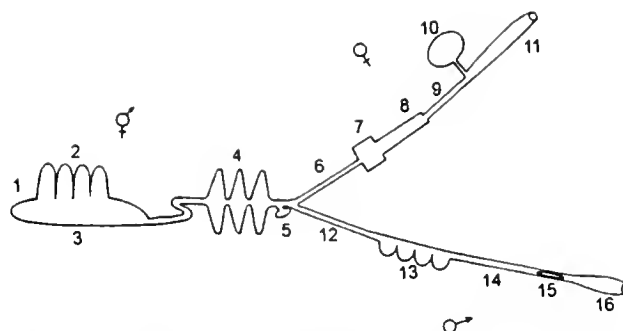


Figure 1. Diagram of the reproductive system of *Biomphalaria tenagophila*. 1. Hind-part of ovotestis; 2. Follicles of the ovotestis; 3. Ovotestis collecting canal; 4. Seminal vesicle; 5. Albumen gland; 6. Oviduct; 7. Muciparous gland; 8. Oothecal gland; 9. Nidamental gland; 10. Spermatheca; 11. Vagina; 12. Spermioviduct; 13. Prostate; 14. Deferens canal; 15. Penis sheath; 16. Preputium

gland, seminal vesicle and ovotestis (Figure 1). Counting in a section of the digestive gland determined the amount of incorporation of radioisotope outside the reproductive system, the background radioisotope incorporation. The ovotestis was macerated releasing material from the collecting canal and follicles. These contents were collected separately from the rest of the macerate. Each sample was transferred to a vial containing 0.3 or 0.5 ml of a solution of 3 % sodium hypochloride (commercial bleach). The material was repeatedly refluxed with a Pasteur pipette until completely dissolved. Preparation of filter paper strips imbibed with samples for measuring in the liquid scintillator was based on the methodology of Byfield and Scherbaum (1966).

Though spermatozoa may be found and counted in different organs of the reproductive system during and after the pairing process (Monteiro and Kawano, 1998), in this work the occurrence of allospermatozoa in the examined organs was accounted for only by counting in the liquid scintillator.

Some controls were used to test the efficiency of the method. Processing of each series of paper strips with samples included a paper strip without sample, a "blank" that allowed us to investigate the amount of free radioactive material that could be absorbed from solutions where the papers with samples were being treated (Table 1).

The radiation in the water where the snail recovered from anesthesia was measured by scintillation to evaluate the efficiency of the inoculation in the lung cavity and the draining of ^3H Td into the medium during the recovery period. The amount of radiation injected into each snail was also measured (Table 1).

RESULTS AND DISCUSSION

The technique of inoculation in the lung cavity through the pneumostome of the anesthetized snail was here used for the first time. The evaluation of this technique

Table 1. Experiments with different supplies of tritiated thymidine (USP and WM supplies)*. Cpm = scintillation counts per minute. Blanks = data not available

| | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 |
|--|--------|--------|--------|--------|
| No. snails | 5 | 5 | 5 | 5 |
| Microliters inoculated/snail | 10USP | 10USP | 10USP | 5WM |
| Inoculation-pairing (days) | 7 | 7 | 11 | 6 |
| Duration of pairing (h) | 24 | 24 | 24 | 24 |
| Pairing-dissection (h) | 52 | 48 | 216 | 40 |
| Separation-dissection (h) | 28 | 24 | 192 | 16 |
| Inoculation to-dissection (approx. days) | 9 | 9 | 20 | 8 |
| Diameter of snails (mm) | 12-14 | 12-13 | 12-13 | 13-14 |
| Reference (cpm) | 27507 | 26911 | 23534 | |
| Background (cpm) | 71 | 65 | 84 | 75 |
| Blank (cpm) | | | 105 | 119 |
| Oviduct (cpm) | 109 | 89 | 78 | |
| Ovotestis collecting canal (cpm) | 91 | 84 | 76 | 105 |
| Follicles of ovotestis (cpm) | 174 | 84 | 107 | 121 |
| Spermatheca (cpm) | 81 | 114 | 114 | 110 |
| Nidamental gland (cpm) | 96 | 890 | 884 | |
| Oothecal gland (cpm) | | | | 135 |
| Seminal vesicle (cpm) | 1184 | 63 | 139 | 121 |
| Digestive gland (cpm) | | 87 | 104 | |
| Carrefour (cpm) | | 76 | 107 | |
| Albumen gland (cpm) | | | | 427 |
| Oviduct -muciparous gland (cpm) | | | | 102 |

* USP, supply kindly offered by Mariano Amabis, University of São Paulo; WM, supply purchased by one of the authors.

was carried out in 18 snails inoculated with a total of 90 μ l of ^3H Td. Retention of inoculate in the lung cavity was tested through measurements of the relative amount of radioisotope that drained during the 4 h recovery from anesthesia. The snails recovered in 27.5 ml of water that yielded 81152.5 cpm. As each 5 μ l of the applied radioisotope solution counted 314850 cpm, there was, on average, a 1.4 % loss of radioactive material from snails to the water. This result encourages the use of this inoculation method in tests of prospective toxicology, selection of mutagens, and of the mechanism of action of water pollutants.

The results of 11 out of a total of 30 experiments are shown in Table 1. The remaining experiments did not record high counts for any of the examined organs. The low counts in all examined organs may have occurred in snails that did not act as females in relation to the inoculated partner. An arbitrary criterion was established: to consider only the experiments in which the counting in the most labeled organ was at least twice as those in the least labeled one.

As a natural consequence of metabolism, the long duration of an experiment might cause the incorporation of the radioisotope in an organ absolutely lacking spermatozoa. This does not seem to be the case here, even in experiments lasting for 216 and 948 h (experiments 3, 10, and 11), from pairing to dissection time. In these conditions, the most labeled organs were the nidamental gland (884 cpm), the albumen gland (210 cpm) and follicles of ovotestis (365 cpm), respectively (Table 1). We looked for possible transfer of the radioisotope label from the reproductive system to a highly metabolically

active organ such as the digestive gland. A fragment of digestive gland, similar in volume to the ovotestis, was simultaneously tested in experiments 2 and 3 (respectively 48 and 216 h after pairing). The relatively low counts, 87 and 104 cpm respectively, discarded that possibility (Table 1).

After a specimen of *B. glabrata* behaves as female during pairing, its spermatheca is packed with spermatozoa. That organ is site of lysis of spermatozoa (Kitajima and Paraense, 1983). Surprisingly, among all the experiments, only one presented relatively elevated countings for spermatheca (206 cpm): experiment 8 (Table 1). Besides, in experiment 9, where the time lapse from pairing to dissection was only 7 h, the spermatheca counting, 87 cpm, was equivalent to the blank (Table 1). Given the countings in the digestive gland (458 cpm), it is possible that the spermatozoa have either bypassed or spent a very brief time in the spermatheca on their way to the digestive gland. Also, due to the relatively short time elapsed from pairing to dissection, 7 h, the hypothesis of radioisotope transfer from spermatheca to digestive gland was not taken into account in the analysis of the data.

No relation was found between the duration of pairing and progression of the allospermatozoa along the reproductive ducts. After only 54 h from the beginning of pairing, in experiment 6, the allospermatozoa were in the follicles of the most distant organ from the vagina, the ovotestis (585 cpm). But 216 h after the beginning of pairing, the allospermatozoa were in the nidamental gland (216 cpm, experiment 3), the organ closest to the vagina (Table 1).

Table 1. Extended.

| Exp. 5 | Exp. 6 | Exp. 7 | Exp. 8 | Exp. 9 | Exp. 10 | Exp. 11 |
|--------|--------|--------|--------|--------|---------|---------|
| 4 | 5 | 3 | 3 | | 3 | 2 |
| 10USP | 5WM | 10WM | 10WM | 10WM | 10WM | 10WM |
| 19 | 7 | 7 | 11 | 19 | 29 | 29 |
| 96 | 24 | 8 | 9 | 6 | 984 | 984 |
| 120 | 54 | 8 | 31 | 6 | | 984 |
| 24 | 30 | 0 | 22 | 0 | ? | 0 |
| 24 | 9 | 7 | 12 | 19 | | 70 |
| 12-14 | 12-14 | 9-13 | 9-11 | 11-12 | 12-13 | 11-12 |
| | 24765 | 24383 | 24357 | 24357 | 24027 | 24585 |
| 75 | 103 | 72 | 99 | 99 | 55 | 65 |
| 119 | 103 | 110 | 87 | 87 | 92 | 77 |
| 103 | 117 | 89 | 76 | 68 | | 68 |
| 787 | 585 | 106 | 89 | 73 | 59 | 365 |
| 168 | 93 | 172 | 206 | 87 | 76 | 147 |
| 133 | 120 | 74 | 77 | 78 | 71 | 84 |
| 111 | 105 | 275 | 74 | 57 | 75 | 68 |
| 115 | 166 | 119 | 92 | 458 | 210 | 63 |
| 314 | 131 | 93 | 84 | 81 | 87 | 65 |

The simultaneous occurrence of high counting in the follicles of ovotestis and in the oviduct-muciparous gland in a single experiment (experiment 5), after 96 h of pairing, suggests the occurrence of double copulation (Dias, 1995). Spermatozoa transferred in the initial copulation could be located in the organ most distant from the vagina, the follicles of ovotestis. The spermatozoa transferred in a subsequent copulation may be located in an organ closer to the vagina, such as the oviduct-muciparous gland (Table 1). This explanation, however, could be inconsistent. Even if the last copulation happened at the end of pairing, the 24 hours that passed after the separation of the partners would be enough for these spermatozoa to advance along the genital tract, bypassing the oviduct-muciparous gland. In a shorter period of time, from pairing to dissection, allospermatozoa proceeded to the seminal vesicle and albumen gland, respectively, in experiments 7 and 9. The results of experiment 3, however, show that it is possible that the spermatozoa remain in the nidamental gland for up to 192 h after the separation of the partners. Therefore, under the experimental conditions, the scintillation counting may indicate that, in a single or in different snails, from a group of 4 (experiment 5, Table 1), the spermatozoa may be located in sites as separated as the ovotestis and organs closer to the vagina such as the oviduct-muciparous gland. It is possible that, rather than suggesting random differences in locomotion ability, these results could indicate strategic, differential placement of allospermatozoa.

All the occurrences of allospermatozoa along the reproductive system, registered in the nidamental gland, seminal vesicle, albumen gland, and follicles of the ovo-

testis are difficult to explain. At first sight, the nidamental gland seems to be a transient site of allospermatozoa on their way to their final destination, where they will fertilize the oocytes (Paraense, 1959). However, their stay in the nidamental gland for 216 h from pairing to dissection time (experiment 3, Table 1), a period of time much longer than that necessary for the spermatozoa to reach the follicles of ovotestis (experiments 5 and 6: 120 h and 54 h, respectively; Table 1), contradicts this premise. Considering that the seminal vesicle of the donor may be empty after pairing (Monteiro and Kawano, 1998), the presence of labeled allospermatozoa in this organ (experiments 1 and 7) suggests that autospermatozoa were replaced by allospermatozoa. This interpretation apparently conflicts with the occurrence of labeled allospermatozoa both in the follicles of ovotestis and in the albumen gland, both within short and long intervals from pairing to dissection (experiments 4, 5, 6, 9, 10, and 11).

No relation was found between the duration of pairing and progression of the allosperm through the reproductive system. The labeled allospermatozoa were located in the spermatheca, nidamental gland, oviduct-muciparous gland, albumen gland, seminal vesicle and follicles of ovotestis. It seems that the destination of allospermatozoa are the follicles of the ovotestis. Their occurrence in the spermatheca, where lysis takes place, may be highly detrimental or fatal. Copulation in *B. tenagophila* may be unilateral or reciprocal (Dias, 1995). Consequently, the length of stay of labeled allospermatozoa in the nidamental gland, oviduct-muciparous gland, or albumen gland may be the result of unilateral copulation, when the snail played only a receiving role, which

resulted in a seminal vesicle full of autospermatozoa. Allospermatozoa may wait within the female tract until the snail plays a donor role in a subsequent pairing, which can be unilateral or reciprocal. Then, allospermatozoa may pass through an empty seminal vesicle toward the follicles of the ovotestis. Within an ovotestis follicle, in the oocyte formation site and co-existing with immature autospermatozoa (Homan, 1972), allospermatozoa may fertilize the oocytes (Laramberg, 1939; Paraense, 1955). The many possible locations for strategic storage of allospermatozoa suggests displacement of autospermatozoa, which makes possible the appropriate deployment of allospermatozoa.

Allospermatozoa were present in ovotestis follicles in experiments 5, 6, and 11, but were not found in the collecting canal of ovotestis in any of the 11 experiments. Notwithstanding, Paraense (1976), labeling snails with ^{59}Fe , found evidence of allospermatozoa in the collecting canal. A possible explanation for this result is the re-incorporation of iron. In fact, the ovotestis has a noted avidity for iron (Heneine *et al.*, 1969; 1970a; 1970b). Of all these locations, the one more consistent with data from the literature is the albumen gland, although all searches for spermatozoa in the canals of the gland and nearby areas during the preparation of the present work have yielded negative results (not even spermatozoa heads were found). Nevertheless, a chamber of fertilization, in the carrefour, next to the albumen gland, is often referred as the final site for storage of spermatozoa in studies carried out on several other species of mollusks (Duncan, 1958; 1960; Lind, 1973; Geraerts and Joosse, 1984).

CONCLUSIONS

Inoculation of a solution of tritiated thymidine through the lung cavity of individuals of *Biomphalaria tenagophila* is an adequate method to label spermatozoa for determining their location in the partner after pairing. Labeled spermatozoa were detected in the receiving snail, through significant levels of scintillation counting, in the spermatheca, seminal vesicle, follicles of ovotestis, nidamental gland, albumen gland, and oviduct-muciparous gland. Material extracted from the collecting canal of the ovotestis did not show countings for labeled spermatozoa. The presence of labeled spermatozoa simultaneously in the follicles of the ovotestis and in the oviduct-muciparous gland suggests options for differential storage locations, in a process that includes displacement of autospermatozoa to allow for adequate positioning of allospermatozoa.

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Status of the tidewater mucket, *Leptodea ochracea* (Say, 1817) (Bivalvia: Unionidae), in Halfway Pond, Massachusetts, USA

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ABSTRACT

The tidewater mucket, *Leptodea ochracea* (Say, 1817), is distributed along the Atlantic coast of North America and is often found on sandy substrates with little or no flow. Halfway Pond, in Plymouth, Massachusetts, is one of the few remaining habitats in Massachusetts for this species, but live specimens have not been collected there since 1981. In summer 1995, the pond was surveyed in an attempt to determine if the tidewater mucket had been extirpated. Of 213 live unionids collected, comprising 6 different species, only 1 specimen was identified as *L. ochracea*. The single specimen was found in the Agawam River outflow area in the southwest corner of the pond along with 4 of the 5 other species of unionids occurring in the pond. This high flow area had a high proportion of benthic macrophytes in a sandy substrate—typical habitat for *L. ochracea*. Other species found in the pond include *Elliptio complanata* (Lightfoot, 1786), *Lampsilis radiata radiata* (Gmelin, 1791), *Alasmidonta undulata* (Say, 1817), *Strophitus undulatus* (Say, 1817), and *Pyganodon cataracta* (Say, 1817). This study confirms the decline of *L. ochracea* in Halfway Pond, Massachusetts, over the last 15 years. If not already gone, this species may disappear from the pond once the remaining individuals die.

Key words: Unionoidea, freshwater clams, freshwater mussels, extirpation

INTRODUCTION

The tidewater mucket, *Leptodea ochracea* (Say, 1817), is a freshwater mussel (family Unionidae) distributed along the Atlantic coast of North America from Nova Scotia to Georgia (Johnson, 1947; 1970; Strayer and Jirka, 1997). Populations are often found on sandy substrates with little or no flow (Smith, 1981), usually in water bodies near the ocean but not necessarily connected to it.

In Massachusetts, *Leptodea ochracea* is found in coastal plain ponds larger than four hectares, along the southeastern portion of the state, from the South Shore to Buzzard's Bay to Cape Cod (Smith, 1991). Because of its highly restricted geographic distribution and de-

creasing abundance in ponds throughout its range, the tidewater mucket is listed as a species of special concern (Smith, 1981; Williams *et al.*, 1993; MDFW, 1997).

Over the past 65 years, *Leptodea ochracea* was found in Halfway Pond in Plymouth County on several occasions (Table 1). Since 1981, however, it has not been recorded there (Nature Conservancy, unpublished data). In the summer of 1995, the author surveyed Halfway Pond in an attempt to determine the distribution status of *L. ochracea* and other unionids.

Halfway Pond is a 94 ha freshwater pond with a 4.9 ha island preserve in its center located just south of Plymouth, Massachusetts, next to Miles Standish State Forest. The island preserve is a candidate for designation as a National Natural Landmark by the Department of the Interior mainly because it contains one of the oldest forests remaining in Massachusetts (Nature Conservancy, unpublished data) and is located in the area with the fastest development rates in the state (Livingston, 1987).

MATERIALS AND METHODS

Live mussels were collected by hand with a meter-long dip net with 2.5 cm mesh. Surveys were supplemented by snorkeling to a depth of 1.5 meters. The net handle was used to delineate a circular quadrat for each sample area (1 m² area). Surveys were conducted at 2 to 4 m intervals; 30 samples were taken at the first 2 sites and 15 samples at the remaining 4 sites around the lake. For each specimen, species name, total length in millimeters, degree of dissolution of the shell (shell wear), collection locality, and sediment type (estimated visually as sand, mud, or cobble) were recorded. Specimens were examined for identification with a 6 × hand lens and dissecting microscope to 30 ×, when necessary. Specimens were only dissected when internal characters were required for identification. Species were identified using Smith (1991) as a primary source and McMahon (1991) and Peekarsky *et al.* (1990) as supplemental sources.

Table 1. *Leptodea ochracea* in Halfway Pond, Massachusetts: specimens in major American museum collections.

| No. specimens | Locality | Collector(s) | Date | Collection No. |
|---------------|-----------------------------------|---|---------------|---|
| 1 | Halfway Pond | ex-MCZ | | USNM 656539 |
| 3 | Halfway Pond | R. I. Johnson | | USNM 592091 |
| 1 | along Mast Road, Halfway Pond | ex-MCZ | [pre-1975] | OSUM 38073 |
| 4.5 | Halfway Pond | R. E. M., W. F. C. (William F. Clapp?) ex-MCZ | Aug. 19, 1933 | OSUM 26550 |
| 9 | Halfway Pond | R. I. Johnson | Jul. 1, 1941 | AMNH 72936, DMNH 48551, USNM 600325 |
| 3 | Halfway Pond outlet | R. I. Johnson | June 1943 | MCZ 134841, MCZ 159150 |
| 4 | Halfway Pond | M. K. Jacobson | Aug. 22, 1952 | AMNH 121013 |
| 4 | South shore, Halfway Pond | M. K. Jacobson | Aug. 23, 1952 | AMNH 127888 |
| 12 | Agawam River outlet, Halfway Pond | D. G. Smith, A. E. Pratt | July 1981 | UMAMZ 539 |

Voucher specimens for *Leptodea ochracea* were not submitted due to the scarcity of specimens.

Over the past 300 years there has been some confusion as to the proper nomenclature of *Leptodea ochracea* (Johnson, 1947; 1970; Morrison, 1975; Bereza and Fuller, 1975), since its original description as *Pectunculus fluviatilis* Lister, 1685. A forthcoming manuscript (Cordeiro, in preparation) should clarify many of the complex nomenclatural issues involving this species. In light of this uncertainty in nomenclature, the author herein will refer to the species as *Leptodea ochracea* (Say, 1817) as per its listing in Turgeon *et al.* (1998).

Institutional abbreviations used are: AMNH, American Museum of Natural History, New York; DMNH, Delaware Museum of Natural History, Greenville, Delaware; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; OSUM, Museum of Biological Diversity, Ohio State University, Columbus, Ohio; UMAMZ, University of Massachusetts Museum of Comparative Zoology, Amherst, Massachusetts; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

RESULTS

The freshwater mussels *Elliptio complanata* (Lightfoot, 1786), *Lampsilis radiata radiata* (Gmelin, 1791), *Alasmodonta undulata* (Say, 1817), *Strophitus undulatus* (Say, 1817), *Pyganodon cataracta* (Say, 1817), and *Leptodea ochracea* were collected along the shores of Halfway Pond and the Halfway Pond Island Preserve. Table 2 depicts results of surveys at the 6 sites around the lake. Survey site 1 is sandy with no benthic, macrophytic plants and frequently used for sport fishing. All mussels collected there were identified as *E. complanata*. Site 2 was also sandy and clear. Only 2 live specimens of *E. complanata* were found. Site 3 had a sandy substrate that was lightly (15%) plant-covered. Forty-seven live specimens of *E. complanata* and 6 *L. radiata radiata* were found. Site 4 was sandy and moderately (50%) plant-covered with 80 live specimens of *E. complanata*, 5 *L. radiata radiata*, and 1 *A. undulata*. Site 5 at the Agawam River outflow was choked with macrophytes amidst occasional spots of bare sand. Although not measured, current flow was estimated to be higher than in the other

Table 2. Sampling results: samples taken, species, and specimen number obtained in surveys of Halfway Pond, Massachusetts.

| Site | Locality | Samples | Species | No. specimens |
|------|---|---------|---------------------------|---------------|
| 1 | 0.3 km S of Mast Rd., west bank | 30 | <i>E. complanata</i> | 14 |
| 2 | N end Mast Rd., northernmost shore | 30 | <i>E. complanata</i> | 2 |
| 3 | NW corner Island | 15 | <i>E. complanata</i> | 47 |
| | Preserve | | <i>L. radiata radiata</i> | 6 |
| 4 | SW shore Island | 15 | <i>E. complanata</i> | 80 |
| | Preserve | | <i>L. radiata radiata</i> | 5 |
| | | | <i>A. undulata</i> | 1 |
| 5 | Agawam River outflow, SW corner | 15 | <i>E. complanata</i> | 22 |
| | | | <i>L. radiata radiata</i> | 2 |
| | | | <i>S. undulatus</i> | 1 |
| | | | <i>P. cataracta</i> | 1 |
| | | | <i>L. ochracea</i> | 1 |
| 6 | SW corner, at pumping station, NW of site 5 | 15 | <i>E. complanata</i> | 31 |

surveyed areas in the pond. Maximum depth was less than 1 m. Twenty-two specimens of *E. complanata*, 2 *L. radiata radiata*, 1 *S. undulatus*, 1 *P. cataracta*, 1 unknown juvenile mussel, and the only specimen of the target species, *L. ochracea*, from the entire survey, were found. The water on survey site 6 was cloudy; the bottom at this site was lightly covered with plants and sandy. Thirty-one specimens plus 1 unknown juvenile were identified as *E. complanata*.

A total of 213 live specimens comprising 6 different species were collected in 6 sites around the lake. All specimens showed evidence of shell dissolution, mostly light wear (nacre exposed on 25% or less of the shell surface). Mean specimen length for *Elliptio complanata*, the only species collected in significant numbers for analysis, was 76.2 mm ($n = 191$), although this figure is most likely inflated due to bias in sampling methodology. At sample site 5, the only area where the target species was found, specimens of *E. complanata* were 11.6% larger than in the other sites. In addition, the greatest diversity (5 species) was found at this site.

DISCUSSION

The density of *Leptodea ochracea*, is decreasing in Halfway Pond. This study confirms general observations of decline over the past 15 years. The single specimen found in this survey is the only documentation of the existence of *L. ochracea* in Halfway Pond since 1981 when Doug G. Smith and A. E. Pratt, University of Massachusetts Museum of Comparative Zoology, collected 12 specimens (UMAMZ 539). Agricultural runoff from nearby cranberry bogs recently contributed to decreased water clarity accompanied by fish kills and potential decrease in mussel density (Douglas G. Smith, personal communication). *Leptodea ochracea* is typically found at low densities across its range in northeastern North America (Smith, 1991; Strayer *et al.*, 1994; Strayer and Smith, 1996; Strayer and Jirka, 1997). The single specimen represents 0.47% of all specimens found ($n = 213$). Strayer *et al.* (1994) found only 33 in their study of the Hudson River estuary in eastern New York and report the species constituting approximately 5% of the unionid community of over one billion animals. Repeated sampling of the same area in 1993–1995, subsequent to zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) invasion, resulted in only 16 specimens found. At the time of this study (1995), zebra mussels had not reached Halfway Pond.

The *Leptodea ochracea* found in this study was in the pond outflow in an area of high benthic macrophyte cover and sandy substrate that is typical habitat for this species (Johnson, 1947; 1970). Increased species diversity in this area (5 of 6 total) and increased mean length of the most common species, *Elliptio complanata*, supports the prevision that the outflow area is a vital microhabitat for freshwater mussels in Halfway Pond. Increased densities of other freshwater mussel species (Nalepa and Gauvin, 1988) and filter-feeding insects (Allan, 1995;

142) have also been observed at other lake outflows. Favorable conditions may include increased nutrient flow across mussel ctenidia induced by the increased stream flow, or protection from fish and mammal predators amidst the macrophytic plants.

Whatever the cause, the Agawam River outflow area is an important refugial microhabitat for the continued survival of *Leptodea ochracea* in Halfway Pond. The outlook for this species in the pond, however, is not good. With such a low density, reproductive potential may not be high enough to maintain a population. Surveys of similar areas in other coastal ponds should be conducted and appropriate protective measures taken if *L. ochracea* is to remain as a species of special concern or upgraded to endangered status in Massachusetts.

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In Memoriam

Ruth D. Turner Rudolf Stohler

1914-2000

1901-2000

Notices

An increase in the subscription rate of *The Nautilus* will take place effective volume 115 (2001). This increase represents an adjustment for the mounting costs of production, printing, and mailing, which in turn reflect inflation rates in the USA integrated during the last 5 years. Our last increase in the subscription rate took place in March of 1995. The increase is much needed if we are to keep following the customary high standards of production, printing, and distribution.

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Sincerely,

José H. Leal, Ph.D.
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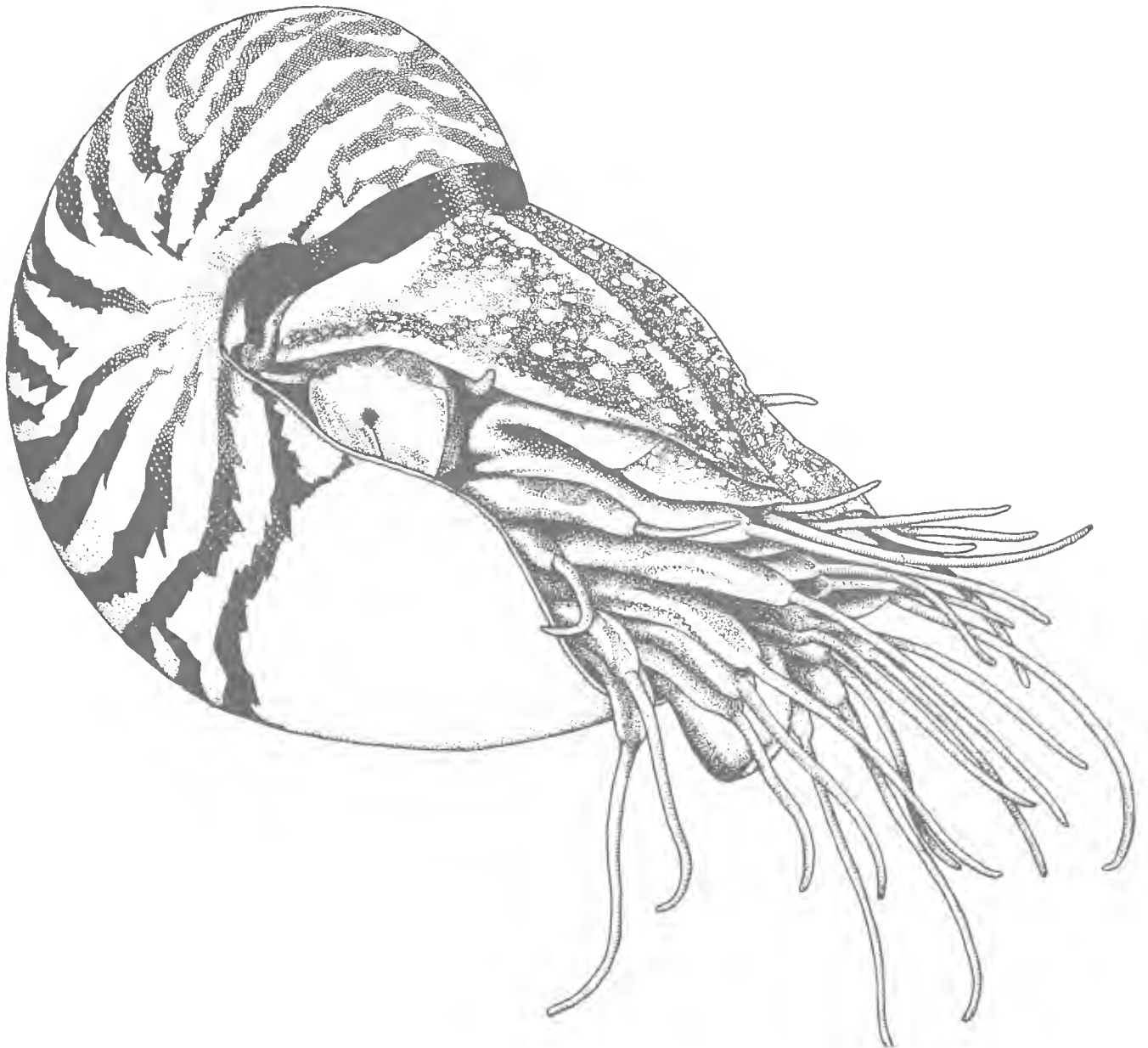
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Phylogeny of some gastropod mollusks derived from 18S rDNA sequences with emphasis on the Euthyneura

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ABSTRACT

The phylogenetic relationships among gastropod subgroups, with emphasis on the Euthyneura, were investigated through the analyses of nearly complete 18S rDNA sequences of 29 representative gastropods. Neighbor-joining, maximum-likelihood, and maximum-parsimony methods were used in the construction of phylogenetic trees. The 18S rDNA data support the monophyly of Vetigastropoda, the vetigastropod clade Trochoidea, and Caenogastropoda. However, the monophyly of two caenogastropod subgroups, Neotaenioglossa and Neogastropoda, are not supported. The basal position of Neritopsina is confirmed. Within the Euthyneura, the Stylommatophora and the Systellommatophora are monophyletic, but the Opisthobranchia, the Pulmonata, and the Basommatophora are not. The present study supports the inclusion of Succineidae within Stylommatophora. However the phylogenetic position of Systellommatophora within Gastropoda remains unresolved.

Additional key words: Mollusca, molecular phylogeny, Apogastropoda, Caenogastropoda, Opisthobranchia, Pulmonata, Vetigastropoda, Stylommatophora, Basommatophora, Systellommatophora, Archaeopulmonata.

INTRODUCTION

Of the molluscan classes, Gastropoda is the most diverse and the most ubiquitous group. It has successfully adapted to most habitats, including marine, freshwater, and terrestrial environments.

Many comparative studies were published based on morpho-anatomical characters, including those of shell, pallial complex, and nervous, reproductive, and digestive systems (for recent reviews, see Haszprunar, 1988a; Bieler, 1992; Ponder and Lindberg, 1997). However, the status of knowledge of the phylogenetic relationships among and within the gastropod subgroups is still controversial (e.g., Golikov and Starobogatov, 1975; Graham, 1985; Haszprunar, 1988a; Bieler, 1992; Ponder and Lindberg, 1996; 1997). This uncertainty is largely due to the lack of informative morphological characters com-

mon to the different taxa and the presence of the high level of phenotypic diversity observed in the Gastropoda.

In addition to morphological characters, molecular sequences have proven to be very useful for in phylogenetic reconstructions. 18S rDNA sequences are amongst the most informative molecular characters along a broad range of taxa within the Mollusca (e.g., Steiner and Müller, 1996; Winnepeninckx *et al.*, 1996; Winnepeninckx *et al.*, 1998a; Winnepeninckx *et al.*, 1998b; Adamkewicz *et al.*, 1997; Bargues and Coma, 1997; Canapa *et al.*, 1999) and other animal phyla. Several studies were published on the molecular phylogeny of Gastropoda based on the sequence data of 28S rDNA (Rosenberg *et al.*, 1994; 1997; Tillier *et al.*, 1994; Tillier *et al.*, 1996) and 18S rDNA (Winnepeninckx *et al.*, 1996; Winnepeninckx *et al.*, 1998a; Harasewych *et al.*, 1997a; b; 1998). Winnepeninckx *et al.* recently (1998a) investigated the phylogeny of gastropod groups below the class rank using the complete 18S rDNA sequences from 18 gastropod species.

To further address gastropod phylogeny with emphasis on Euthyneura (Opisthobranchia + Pulmonata), a group that has not been examined or discussed in detail from 18S rDNA data, we determined the complete 18S rDNA sequences for five representative gastropods. They include the first complete sequence data from Cephalaspidea (within Opisthobranchia) and Archaeopulmonata (within Pulmonata), and additional sequence data from Vetigastropoda and Stylommatophora (this latter within Pulmonata). These sequences were analyzed in conjunction with previously published sequences of 24 other gastropods. We focus on testing the monophyly of each of the euthyneuran subgroups, the Opisthobranchia (e.g., Boettger, 1955; Ghiselin, 1965; Gosliner, 1981; 1985; 1991; Gosliner and Ghiselin, 1984; Poulicek *et al.*, 1991; Ponder and Lindberg, 1997), the Basommatophora (e.g., Tillier, 1984; Haszprunar and Huber, 1990; Nordsieck, 1992), the Stylommatophora (e.g., Nordsieck, 1992), and the Systellommatophora (Sakini-Plavén, 1980; Climo, 1980; Tillier, 1984; Haszprunar and Huber, 1990; Nordsieck, 1992). We also discuss the phy-

¹ Author for correspondence.

logenetic position of the Succineidae in the Stylommatophora (Rigby, 1965; Solem, 1978; Tillier, 1989; Nord-sieck, 1992). In addition, we examine the monophylies of the Vetigastropoda (Salvini-Plawen, 1980; Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a; b; Ponder and Lindberg, 1996) and the vetigastropod clade Trochoidea (Haszprunar, 1988a).

MATERIALS AND METHODS

SPECIMENS ANALYZED

The 18S rDNA sequences of two vetigastropods (*Nordotis discus*, 1858 base pairs, from Cheju Island and *Batillus cornutus*, 1859 base pairs, from Mara Island), one opisthobranch (*Bullacta exarata*, 1849 base pairs, from Inchon), and two pulmonates (*Ellobium chinensis*, 1845 base pairs, from Tamjin River, and *Acusta despecta sieboldiana*, 1847 base pairs, from the Campus of Seoul National University). The material above was collected in Korea, and their sequences are described for the first time in the present study. The sequences of two neogastropods (*Rapana venosa* and *Reishia bronni*), one pulmonate (*Anthosiphonaria sirius*), and one chiton (*Lepidozona (Lepidozona) coreanica*) were reported in our previous study (Yoon *et al.*, 1996) and the sequences of the remaining 21 other gastropods and 2 bivalves were obtained from GenBank.

The nearly complete 18S rDNA sequences were analyzed for the 29 representative gastropods (one neritoid, three vetigastropods, nine caenogastropods, two opisthobranchs, and 14 pulmonates), two bivalves, and one chiton species. Of these, the polyplacophoran *Lepidozona (Lepidozona) coreanica* was used as an outgroup, as the class Polyplacophora (included in the Aculifera) is currently accepted as the stem group of the classes Gastropoda and Bivalvia (included in Conchifera), from studies based on morphological characters (see Salvini-Plawen, 1980; 1990; Haas, 1981; Runnegar and Pojeta, 1985; Brusca and Brusca, 1990; Ponder and Lindberg, 1996) as well as molecular results (Adamkiewicz *et al.*, 1997; Bargues and Mas-Coma, 1997; Hara-sewych *et al.*, 1997b). Table 1 lists the studied taxa and GenBank accession numbers for the respective sequences. The baseline classification used in this work follows Haszprunar (1988a) for Streptoneura, Vaught (1989) for Opisthobranchia, and Boss (1982) for Pulmonata.

DNA EXTRACTION, PCR AMPLIFICATION, AND SEQUENCING

Total nucleic acids were extracted from foot muscle of live-collected and ethanol-preserved snails by modifications of standard procedure of Sambrook *et al.* (1989). The 18S rDNAs were amplified using the polymerase chain reaction (PCR) with two oligonucleotide primers corresponding to conserved sequences proximal to 5' and 3' termini of metazoans (Nelles *et al.*, 1984: 1–19, 5'-CCTGGTTGATCCTGCCAG-3'; 1848–1868, 5'-TAATGATCCTTCCGCAGGTTA-3'; the numbers cor-

Table 1. Gastropod species used in the present study, with GenBank accession numbers for sequences.

| | |
|---------------------------------|------------------------------------|
| NERITOPSINA | APLYSIOMORPHA |
| NERITOIDEA | APLYSIOIDEA |
| Neritidae | Aplysiidae |
| <i>Nerita albicilla</i> X91971 | <i>Aplysia</i> sp. X94268 |
| VETIGASTROPODA | PULMONATA |
| HALIOTOIDEA | ARCHAEOPULMONATA |
| Haliotidae | ELLOBOIDEA |
| * <i>Nordotis discus</i> | Ellobiidae |
| AF082177 | * <i>Ellobium chinensis</i> |
| TROCHOIDEA | AF190452 |
| Trochidae | BASOMMATOPHORA |
| <i>Monodonta labio</i> X94271 | SIPHONARIOIDEA |
| Turbinidae | Siphonariidae |
| * <i>Batillus cornutus</i> | <i>Anthosiphonaria sirius</i> |
| AF165311 | X98828 |
| CAENOASTROPODA | <i>Siphonaria algesirae</i> |
| NEOTAENIOGLOSSA | X91973 |
| LITTORINOIDEA | LYMNAEOIDEA |
| Littorinidae | Lymnaeidae |
| <i>Littorina littorea</i> | <i>Lymnaea glabra</i> Z73982 |
| X91970 | <i>Bakerilymnaea cubensis</i> |
| <i>Nodilittorina punctata</i> | Z83831 |
| Y11755 | STYLOMMATOPHORA |
| CALYPTRAEOIDEA | MEASURETHRA |
| Calyptraeidae | CLAUSILIOIDEA |
| <i>Crepidula adunca</i> | Clausiliidae |
| X94277 | <i>Balca biplicata</i> X94278 |
| TONNOIDEA | HETERURETHRA |
| Bursidae | Succineidae |
| <i>Bursa rana</i> X94269 | <i>Oxyloma</i> sp. X94276 |
| NEOGASTROPODA | <i>Omalyonx matheroni</i> |
| MURICOIDEA | AF047199 |
| Muricidae | Athoracophoridae |
| <i>Reishia bronni</i> X98827 | <i>Athoracophorus bitent-</i> |
| <i>Rapana venosa</i> X98826 | <i>culatus</i> AF047198 |
| Buccinidae | SIGMURETHRA |
| <i>Pisania striata</i> X94272 | ACHATINOIDEA |
| Nassariidae | Achatinidae |
| <i>Nassarius singuijorensis</i> | <i>Limicolaria kambeul</i> |
| X94273 | X66374 |
| Fascioliidae | HELICOIDEA |
| <i>Fasciolaria lignaria</i> | Bradybaenidae |
| X94275 | * <i>Acusta despecta sieboldi-</i> |
| EUTHYNEURA | <i>ana</i> AF190453 |
| OPISTHOBRANCHIA | Helicidae |
| CEPHALASPIDEA | <i>Helix aspersa</i> X91976 |
| PHILINOIDEA | SYSTELLOMMATOPHO- |
| Hamineidae | RA |
| * <i>Bullacta exarta</i> | ONCHIDIOIDEA |
| AF188675 | Onchidiidae |
| | <i>Onchidella celtica</i> |
| | X70211 |
| | VERONICELLOIDEA |
| | Veronicellidae |
| | <i>Laevicaulis alte</i> X94270 |

Note: Classification follows Haszprunar (1988a) for Streptoneura, Vaught (1989) for Opisthobranchia, and Boss (1982) for Pulmonata. * New sequences marked with asterisk.

respond to positions of human 18S rDNA). PCR amplifications were performed with Taq DNA polymerase for 30 cycles (94° C for 1 min, 52° C for 2 min, and 72° C for 3 min). The ends of the amplified DNA fragments were modified for blunt-ended ligation using T4 kinase and T4 polymerase. The blunt-ended 18S rDNAs were ligated into pGEM-3zf(-) plasmid vector and transformed into DH5- α cell lines. Sequencing primers used in this study were reported in a previous paper (Moon *et al.*, 1996). 18S rRNA-coding regions were completely sequenced in both directions with complete overlap. The DNA sequencing was performed by the dideoxynucleotide chain-termination method (Sanger *et al.*, 1977) using a Taq-Track kit (Promega Co.), according to the manufacturer's instructions. Electrophoresis of sequencing reaction mixtures was performed on buffer-gradient 6% polyacrylamide gels and examined by autoradiography.

PHYLOGENETIC ANALYSIS OF 18S rDNA SEQUENCES

The sequences were initially aligned with the CLUSTAL W multiple-alignment program (Thompson *et al.*, 1994) and the alignment refined manually. A data-set of alignment-stable positions was produced by excluding those positions that differed between alignments (Gatesy *et al.*, 1993). Analyses were limited to reliably aligned regions, which included a total of 1754 nucleotide positions. Phylogenetic reconstructions were performed using the neighbor-joining (NJ), maximum-likelihood (ML), and maximum-parsimony (MP) methods. PHYLIP version 3.572c (Felsenstein, 1995) was used for the neighbor-joining (Saitou and Nei, 1987) analyses. The distance analyses were done using Kimura (1980) and Jukes and Cantor (1969) matrices as input for the neighbor-joining analyses. Maximum-likelihood analyses were performed using the HKY (Hasegawa *et al.*, 1985) model in PAUP 4.0b2 (Swofford, 1999). For the quartet puzzling method (the number of puzzling steps is 1000), empirical nucleotide frequencies, and transition/transversion ratio of 1.5 were estimated. Parsimony analyses were also performed using the computer program PAUP version 4.0b2 with closest stepwise addition options. The analyses employed a heuristic search using TBR branch swapping with random taxon addition. Branch length was optimized according to the ACCTRAN option. Bootstrap analyses (Felsenstein, 1985) of one hundred replicates were performed to examine the confidence of nodes in NJ, ML, and MP analyses.

RESULTS

Figure 1A shows the phylogenetic tree resulting from the neighbor-joining (NJ) analysis using the Kimura (1980) distances of an alignment of complete 18S rDNA sequences of 29 gastropod species. The polyplacophoran *Lepidozona* (*Lepidozona*) *coreanica* was used as out-group. The same tree topology was also obtained using Jukes and Cantor (1969) distances. The Neritoidea

branches off first and the Vetigastropoda (Trochoidea + Haliotoidea) diverges next as an independent clade before the clade Apogastropoda (Caenogastropoda + Euthyneura). The monophyly of the Vetigastropoda and its subclade the Trochoidea (represented by *Monodonta* and *Batillus*) is clearly shown in the tree, with very high bootstrap support (100%: 100%). The Caenogastropoda shows a sister group relationship with the Euthyneura with very high bootstrap support (94%). Monophyly of the Caenogastropoda is supported (bootstrap value = 100%), though neither the Neotaenioglossa (= Mesogastropoda) nor the Neogastropoda emerged as monophyletic clades.

There is strong bootstrap support (100%) for the monophyly of Euthyneura (Opisthobranchia + Pulmonata), though the monophyly of Opisthobranchia (Cephalaspidea + Anaspiioidea) and Pulmonata are not supported. The Basommatophora, consisting of the Siphonarioidea and Lymnaeoidea, did not emerge as a monophyletic group. On the other hand, there is good support for the monophyly of two additional groups in the Euthyneura, the Stylommatophora (bootstrap value = 84%) and the Systellommatophora (bootstrap value = 87%). Bootstrap values strongly support the position of the Succineidae (*Oxyloma* and *Omalonyx*) within the stylommatophoran clade. However, the position of the Systellommatophora within the Gastropoda was not positively determined in the present study.

The resulting tree from maximum-likelihood (ML) analyses of the same data set is shown in figure 1B. The ML tree confirms all the major results of the NJ tree (figure 1A), with the exception that clades within Euthyneura lack significant bootstrap-support. The new branching order of Systellommatophora (*Onchidella* and *Laevicaulis*), Aplysiomorpha (*Aplysia*), Archaeopulmonata (*Ellobium*)–Siphonarioidea (*Siphonaria* and *Anthosiphonaria*), Cephalaspidea (*Bullacta*), and Stylommatophora in the clade differs from the order shown in the NJ tree (figure 1A), Aplysiomorpha–Systellommatophora–Siphonarioidea and Archaeopulmonata–Cephalaspidea–Stylommatophora.

The maximum parsimony (MP) analyses produced a single tree with minimum length of 950 steps (figure 1C). Generally speaking, MP analyses also yielded similar results except for minor differences in topologies among groups within the caenogastropod and the euthyneuran clades. Maximum parsimony shows topological shifts within the caenogastropod clade, e.g., the new branching order of *Bursa*, *Nassarius*, and *Pisania*–*Fasciolaria*–*Crepidula* instead of the order shown in the NJ tree (figure 1A), *Crepidula*, *Bursa*, *Pisania*, *Nassarius*, and *Fasciolaria*. Within the Euthyneura, the MP tree differs from the NJ tree only in those branching points with low bootstrap values. There is no sister-group relationship among the Cephalaspidea (*Bullacta*), Aplysiomorpha (*Aplysia*), Archaeopulmonata (*Ellobium*), Siphonarioidea, Stylommatophora, and Systellommatophora.

Next, we focused on the Euthyneura in separate,

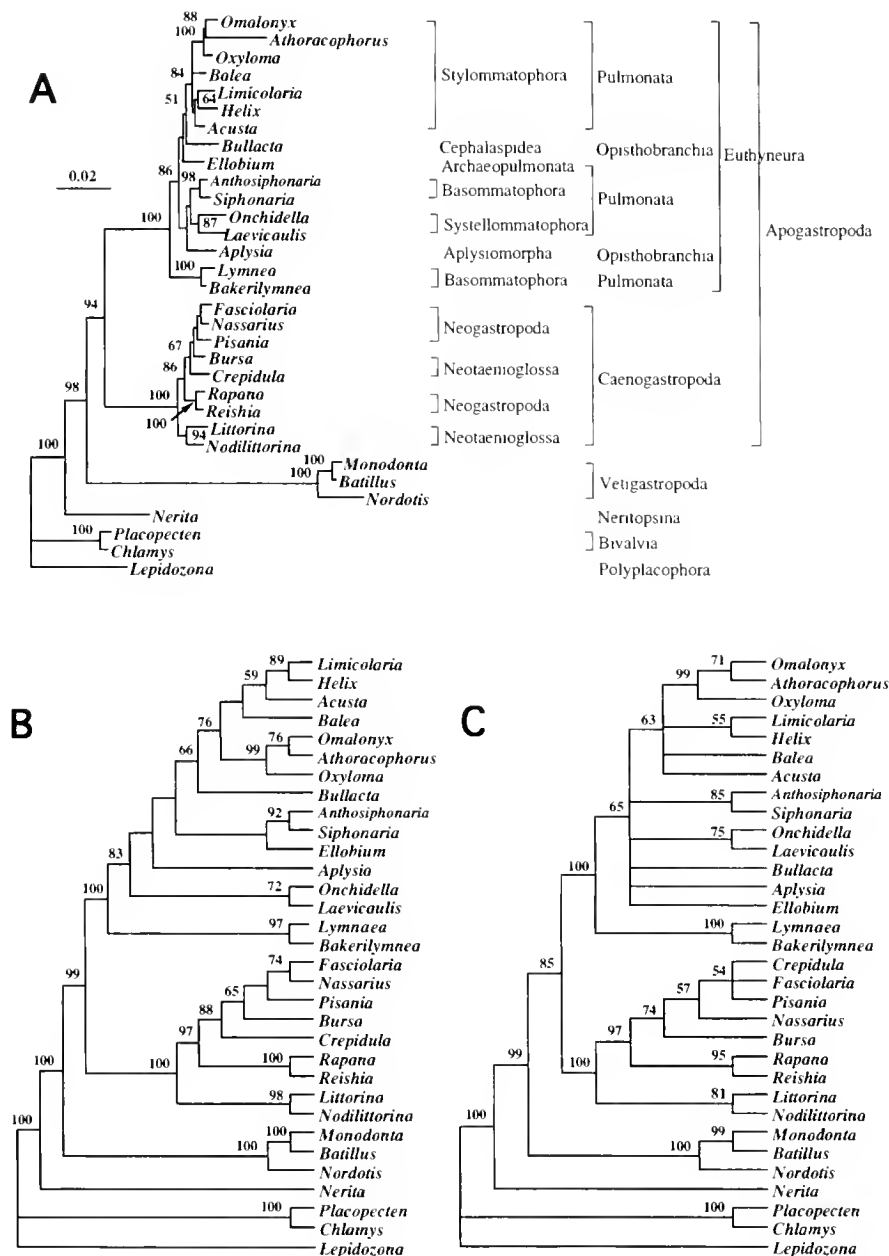
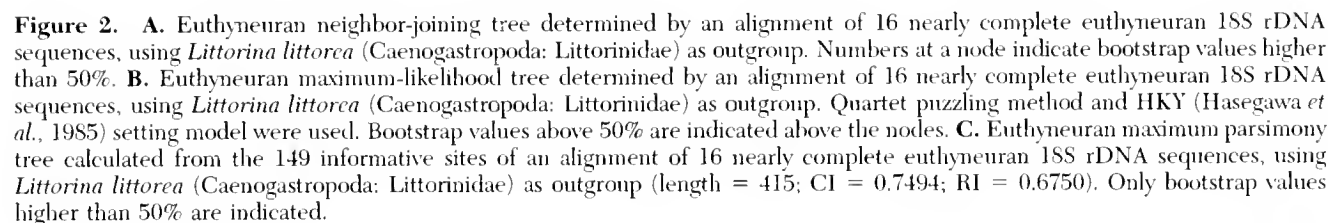


Figure 1. **A.** Neighbor-joining tree determined by an alignment of 29 nearly complete 18S rDNA sequence data for gastropods with *Lepidozona coreanica* (Polyplacophora) as outgroup. Bootstrap percentages are shown above branches supported in at least 50% of 100 replicates. **B.** Strict consensus tree resulting from maximum-likelihood analyses of 29 nearly complete gastropod 18S rDNA sequences. Quartet puzzling method and HKY (Hasegawa *et al.*, 1985) setting model were used. *Lepidozona coreanica* (Polyplacophora) was the outgroup. Bootstrap analysis was performed with 100 replicates; values above 50% are indicated above the nodes. **C.** Strict consensus tree of maximum parsimony analyses based on the 333 informative sites of an alignment of 29 nearly complete gastropod 18S rDNA sequences (length = 950; C1 = 0.6611; R1 = 0.8418). *Lepidozona coreanica* (Polyplacophora) was the outgroup. Bootstrap values higher than 50% are indicated above the nodes.

mainly because the use of outgroups that are too far removed from the clade in study may give origin to additional homoplasies between ingroup and outgroup species. Figure 2A shows the results of NJ analyses of 16 nearly complete euthyneuran 18S rDNA sequences, with the caenogastropod *Littorina littorea* as outgroup.

The resulting tree exhibits the same topology as the complete NJ tree (figure 1A), with the exception that *Ellobium* (Archaeopulmonata) becomes the sister group to the clade Aplysiomorpha (*Aplysia*) + Systellommatophora-Siphonarioidea, instead of clade Cephalaspidea (*Bullacta*) + Stylommatophora, as present in the com-



nodes are very low. Nevertheless, the euthyneuran ML tree strongly supported most of the major nodes found in the entire ML tree, with generally higher bootstrap values. Maximum parsimony analyses based on the 149 phylogenetically informative characters of the alignment of 16 euthyneuran species produced a single tree with minimum length of 415 steps (figure 2C). In the euthyneuran MP tree, the first branching member is Cephalaspidea (*Bullacta*) rather than Lymnaeoidea (Basomatophora) found in the entire MP tree. The topologies

for the remaining taxa are generally identical to the ones in the tree containing all taxa. The euthyneuran trees resulting from NJ, ML, and MP analyses confirmed the topology of trees generated from the same types of analyses but based on all taxa.

DISCUSSION

For the phylogenetic relationships among and within the gastropod major subgroups, our study supports several aspects of the study by Winnepenickx *et al.* (1998a). The Neritoidea diverged first, followed by the Vetigastropoda. Next, the clade Apogastropoda, comprising the Caenogastropoda and Euthyneura (each well supported as monophyletic groups), appears as a monophyletic group. However, the Neotaenioglossa (= Mesogastropoda) and the Neogastropoda (included in Caenogastropoda) and the Pulmonata (included in Euthyneura) do not appear as monophyletic groups. In addition, the position of Systellommatophora within the Gastropoda could not be defined in the present study.

In contrast to previous reports, our study provides more details on gastropod phylogeny, especially with regard to the phylogenetic status of the subgroups within the Euthyneura. All trees resulting from NJ, ML, and MP analyses refute the monophyly of the Opisthobranchia. This result supports the claims of many opisthobranch workers, whom observed that parallelism and convergence have occurred in most major organ systems within the opisthobranchs (Ghiselin, 1965; Gosliner, 1981; 1985; 1991; Gosliner and Ghiselin, 1984; Poulicek *et al.*, 1991) and that the high degree of homoplasy in many characters in opisthobranchs contribute to difficulties in obtaining robust results from cladistic analyses (Gosliner and Ghiselin, 1984; Gosliner, 1985; 1991). Boettger (1955) maintained that the Opisthobranchia is paraphyletic. Ponder and Lindberg (1997) also suggested that the Opisthobranchia is not monophyletic, a viewpoint in agreement with the results of Tillier *et al.* (1994) from 28S rDNA data. It is not surprising, therefore, that many contradictory phylogenies and classification schemes have been suggested for the Opisthobranchia (e.g., Boettger, 1955; Taylor and Sohl, 1962; Ghiselin, 1965).

In relation to the phylogeny of the Pulmonata, we have mentioned that the Basommatophora (*sensu* Haszprunar and Huber, 1990, Siphonarioidea + Lymnaeoidea), is not monophyletic. Tillier (1984) considered that only Lymnaeoidea belongs to Basommatophora and Siphonarioidea to Archaeopulmonata. He suggested that pulmonates radiated into freshwater habitats as Basommatophora and into marine habitats as Archaeopulmonata. Tillier *et al.* (1996), based on 28S rDNA data, showed that the Basommatophora is not monophyletic. However, Haszprunar and Huber (1990) suggested that both Siphonarioidea and Lymnaeoidea could be allocated in Basommatophora due to the presence of common morphological characters such as a procerebrum comprising only large cells, the lack of a contractile pneu-

mostome, and the presence of an osphradium and pallial ciliary tracts. Nordsieck (1992) based on the presence of an anal opening shifted to the posterior mantle lobe, also considered the marine Thalassophila (Siphonarioidea) to be the sister group of the limnic Hygrophila (Lymnaeoidea). Therefore, the common morphological characters found in the Basommatophoran, rather than representing synapomorphies, could all have been derived by convergence. Nordsieck (1992), based on morphological characters found in tentacles, kidney, central nervous system, and aspects of ontogeny, considered the Stylommatophora to be a monophyletic group, which is concordance with the results derived from 28S rDNA sequence data (Rosenberg *et al.*, 1994; 1997; Tillier *et al.*, 1994; Tillier *et al.*, 1996). Although there is instability of branching pattern, the results for the euthyneuran clade in the present study indicate that the Succineidae (represented by *Oxyloma* and *Omalonyx*) belongs to the Stylommatophora (e.g., Solem, 1978; Tillier, 1989; Nordsieck, 1992). These results, however, contradict the view of Rigby (1965) whom, on the basis of morphological similarities of the digestive and reproductive systems, allocated the Succineidae in the Opisthobranchia. Synapomorphic characters such as the more or less reduced shell and mantle, and a visceral ganglion situated centrally or on the left side with respect to the axis of the central nervous system (e.g., Salvini-Plawen, 1980; Nordsieck, 1992) support the monophyly of the Systellommatophora (represented by Onchidiidae and Veronicellidae). However, this monophyly has been questioned by several authors (e.g., Climo, 1980; Tillier, 1984; Haszprunar and Huber, 1990). Climo (1980) in particular considered the systellommatophorans as a polyphyletic assemblage diverging at the base of the euthyneurans. Tillier (1984) studied the morpho-anatomical characters of the pallial complex, digestive tract, reproductive, and central nervous systems, and divided the Pulmonata into only three orders: Archaeopulmonata, Basommatophora, and Stylommatophora. He included the Systellommatophora in the Archaeopulmonata and suggested that the Onchidiidae (within Systellommatophora) is more closely related to the Ellobiidae (within Archaeopulmonata) than to the Veronicellidae (within Systellommatophora). However, our present result supports the monophyly of Systellommatophora.

Since the erection of the Vetigastropoda by Salvini-Plawen (1980), the presence of synapomorphic characters such as ctenidial sense organs, the epipodial sense organs, and the special structure of the esophagus have generally supported the monophyly of this clade (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a; b; Ponder and Lindberg, 1996; 1997). Other vetigastropod features include the dominant presence of the right dorsoventral retractor muscle, the right excretory organ, and bilamellate ctenidia with skeletal rods. Previous molecular data using partial 18S rDNA (Harasewych *et al.*, 1997a; b) and the 28S rDNA (Tillier *et al.*, 1994) sequences also supported the monophyly of the Vetigastropoda, which is also supported in the present study.

Monophyly of the Trochoidea (represented by *Monodonta* and *Batillus*) is also confirmed herein. The Trochoidea is defined by synapomorphies such as loss of the right etenidium in relation to the loss of the shell slit (Haszprunar, 1988a; b) and the monophyly of the group is also in concordance with the study based on 28S rDNA sequences by Tillier *et al.* (1994).

In conclusion, the 18S rDNA data strongly support the monophyly of the following higher gastropod clades: Vetigastropoda, Trochoidea (within Vetigastropoda), Apogastropoda, and the two included clades Caenogastropoda and Euthyneura. Within the euthyneuran clade, both the Stylommatophora and the Systellommatophora are monophyletic. However, our 18S rDNA data failed to support monophyly of the Neotaenioglossa and the Neogastropoda (within Caenogastropoda), Opisthobranchia, Pulmonata, and the pulmonate Basommatophora. These non-monophyletic subgroups, therefore, at present can be considered as grades rather than clades. The basal position of Neritopsina is confirmed in this study. In addition, the Succineidae is included in Stylommatophora. Still, the Systellommatophoran position within the Gastropoda, that is, its immediate relationship to either Opisthobranchia or Pulmonata, or to any other group for that matter, could not be defined. The instability of topology and short branch lengths within the Caenogastropoda and the Euthyneura may be due to the fact that the mollusks, including gastropods, apparently radiated in an "explosive" fashion during a relatively short period of time. Most extant major groups of mollusks appeared around a relatively short time at the Precambrian/Cambrian boundary (e.g., Runnegar and Pojeta, 1985; Winnepeinnickx *et al.*, 1996; Adamkewicz *et al.*, 1997; Harasevych *et al.*, 1997a). Future studies attempting to define phylogenetic relationships at these levels may take into consideration other molecules such as cytochrome *c* oxidase I and/or 16S rDNA. Such molecules evolve more rapidly than 18S rDNA, and seem more likely to contain information needed to solve phylogenetic relationships within these clades.

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Size-depth patterns in two bathyal turrid gastropods: *Benthomangelia antonia* (Dall) and *Oenopota ovalis* (Friele)

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ABSTRACT

During the past decade, there has been a resurgence of interest in the evolutionary and ecological significance of animal body size. Geographic patterns of body size in deep-sea organisms remain poorly described. In this paper, we analyze depth-related trends of larval and adult shell size in two turrids (Gastropoda) from the western North Atlantic. The upper bathyal *Oenopota ovalis* (478–2022 m), which has non-planktotrophic development, shows significant positive size-depth clines for larval, but not adult shells. The lower bathyal *Benthomangelia antonia* (2359–3834 m), with planktotrophic development, shows no trend for larval shells, but a positive relationship of size to depth for adult shells. The increase in size with depth confirms earlier observations of size-depth clines in deep-sea snails, which may reflect selection for greater competitive ability and foraging efficiency with increased depth. Contrasts in clinal variation between larval and adult shells suggest that different stages of life history in deep-sea snails may respond independently to environmental gradients.

Additional key words: Gastropoda, Turridae, deep sea, size-depth patterns, western North Atlantic.

INTRODUCTION

Animal body size has been related to a wide range of physiological (Peters, 1983; Chown and Gaston, 1999), evolutionary (Stanley, 1979), and ecological phenomena (LaBarbera, 1989). There is also considerable new interest in the implications of body size for geographic range (Brown, 1995), species diversity (Finlay *et al.*, 1996; Nee and Lawton, 1996), abundance (Siemann *et al.*, 1996) and conservation of biodiversity (May, 1988; Marquet *et al.*, 1990; Gaston and Blackburn, 1996). One of the most striking characteristics of the deep-sea fauna, including mollusks, is the small size of most organisms. Explanations for this have centered primarily on measuring size-depth trends in various deep-sea taxa or functional groups, and relating these to food availability, which decreases with depth (Thiel, 1975, 1979; Gage

and Tyler, 1991). Size-depth relationships appear to vary considerably among faunal components (Rex and Etter, 1998). It is unclear the degree to which this inconsistency represents biologically meaningful differences in how organisms respond to environmental gradients, or methodological differences associated with how size is measured and the way that morphologically and taxonomically heterogeneous groups of species have been combined to obtain composite estimates of size. To study size as an adaptation, it is important to standardize measurements to common growth stages and to examine patterns within species (Gould, 1969; Rex and Etter, 1998).

Rex (1979) and Rex and Etter (1990, 1998) showed that size, standardized to specific larval and adult growth stages within individual deep-sea snail species, shows a strong tendency to increase with depth. These studies were based on average interpopulation size differences using relatively few sampling sites, often located near the extremes of the species' depth ranges. Here, we present detailed analyses of size-depth trends in populations of two species of deep-sea snails, using larger sample sizes and much more thorough depth coverage. Results generally support the positive size-depth trends reported earlier, but also suggest that larvae and adults may respond differently to selective differences associated with change in depth.

MATERIALS AND METHODS

This study focuses on two common and taxonomically well-known bathyal turrids, *Benthomangelia antonia* (Dall, 1881) and *Oenopota ovalis* (Friele, 1877), shown in figures 1–4. They were collected from the western North Atlantic, south of New England (table 1, figure 5), using epibenthic sleds (Hessler and Sanders, 1967), box cores (Hessler and Jumars, 1974), Blake deep-sea trawls or beam trawls (Tanner, 1897). The two species were chosen primarily because they were abundant enough in existing collections to allow reasonable statistical analyses across broad depth ranges.

B. antonia and *O. ovalis* differ in their mode of de-

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Figure 1. SEM of the adult shell of *Oenopota ovalis* (Station 87, 1102 m, 4.01 mm total length). **Figure 2.** SEM of the adult shell of *Benthomangelia antonia* (Station 76, 2862 m, 6.51 mm total length). **Figure 3.** SEM of the larval shell of *Oenopota ovalis* (Station 87, 1102m, 0.45mm protoconch height). The indentation before the first readily detectable adult rib (at a magnification of 30 \times) was used as the larval-adult transition (see text for further discussion). **Figure 4.** SEM of the larval shell of *Benthomangelia antonia* (Station 76, 2862 m, 1.18 mm protoconch height). Horizontal arrow indicates the larval-adult transition (see text for further discussion).

velopment (Bouchet and Warén, 1980). *O. ovalis* appears to have direct or lecithotrophic development in which larvae mature in a protected egg capsule and either emerge crawling or undergo a brief pelagic or demersal dispersal phase (e.g., Thorson 1935, 1944; Bouchet and Warén, 1980; Shimek, 1983). In *B. antonia*, larvae hatch at a small size and develop planktotrophically. Veligers evidently undergo ontogenetic vertical migration in the water column, and consequently have more dispersal potential than do the larvae of *O. ovalis* (Killingley and Rex, 1985). An increase in the proportion of species that have planktotrophic development with increased depth seems to be a general pattern in deep-sea turrids of the western and eastern North Atlantic (Potter and Rex, 1992).

Mollusks are useful for this type of study because their calcareous shells record the life history of each individual, and are not subject to the changes in form that are caused by preservation in soft-bodied organisms. We

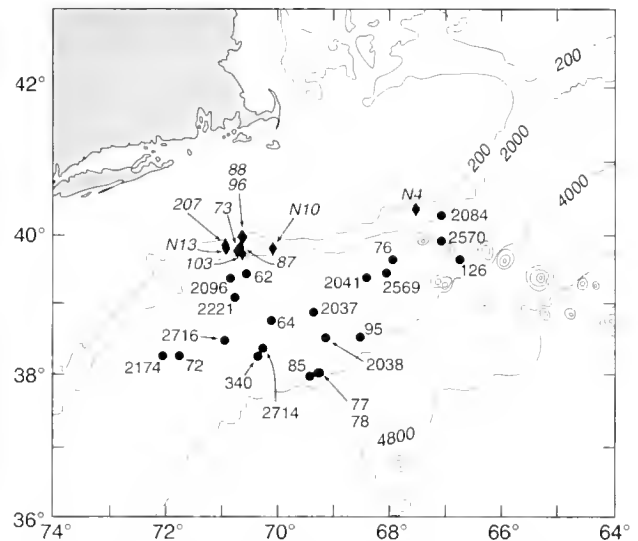


Figure 5. Map of Northwest Atlantic showing the localities of collection stations. See table 1 for station data. Depth contours are in meters. Diamonds represent stations where *Oenopota ovalis* was collected; circles represent sites for *Benthomangelia antonia*.

chose only specimens that were collected live. Measurements of size were standardized to the transition between larval and adult shells (figures 3 and 4). If this was undetectable due to erosion or breaking, the specimen was not used. In *B. antonia*, the transition is clearly marked by changes in both color and sculpture (Bouchet and Warén, 1980; Rex and Etter, 1990). In *O. ovalis*, both larvae and adults are heavily calcified and are the same white color making the transition less distinct. The protoconch is smooth and the adult shell has fine vertical ribs. We used the indentation before the first readily detectable adult rib as the larval-adult transition for this species.

Shells were measured microscopically, orienting them by the method described in Rex and Etter (1990). Each shell was mounted on a disk of clay and then placed on a 4-dimensional stage of an Olympus dissecting microscope equipped with a Sony 3 CCD Color Video Camera mount. The camera was attached to a NuVista Imaging Board in a Macintosh Centris 650 computer. Using NuVista Capture+ Software, the images of the mounted shells were digitized. The saved images were then loaded into the NIH Image program. Previously digitized images of a 1.0 mm stage micrometer with 0.01 mm gradations were used to calibrate and measure the shell images.

Size-depth trends in the two species were analyzed using three variables: standardized larval and adult size, and estimates of final size attained. Early protoconch whorls for one species, *B. antonia*, were often corroded, making it impossible to accurately measure protoconch height in all specimens. Consequently, larval size was taken as protoconch width. Standardized adult size, hereafter referred to as Whorl-1 Size, was measured as

Table 1. Station data for samples of *O. ovalis* and *B. antonia* measured in this study. The species collected, sampling methodology, and number of specimens used in this study are also given. For sampling method: ES = epibenthic sled (Hessler and Sanders, 1967), BC = box core (Hessler and Jumars, 1974), BT = beam trawl, DST = Blake deep-sea trawl (Tanner, 1997). ACSR indicates Atlantic Continental Slope and Rise Study (Maciolek *et al.*, 1986).

| Species | Station | Cruise | Depth (m) | Latitude °N | Longitude °W | Sampling method | Number of individuals |
|-------------------------------|---------|-----------|--------------|-------------|--------------|--------------------|--------------------------|
| <i>Oenopota ovalis</i> | 88 | CHAIN | 475 | 39°54.10' | 70°37.00' | ES | 3 |
| | 96 | CHAIN | 495 | 39°55.20' | 70°39.50' | ES | 3 |
| | N4 | ACSR | 550 | 40°21.17' | 67°32.15' | BC | 1 |
| | 207 | CHAIN | 505 | 39°51.15' | 70°55.35' | ES | 6 |
| | 57 | CHAIN | 1102 | 39°45.70' | 70°40.50' | ES | 29 |
| | N10 | ACSR | 1220 | 39°45.10' | 70°05.30' | BC | 2 |
| | N13 | ACSR | 1250 | 39°45.35' | 70°54.94' | BC | 1 |
| | N13 | ACSR | 1250 | 39°45.35' | 70°54.94' | BC | 1 |
| | 73 | ATLANTIS | 1400 | 39°46.50' | 70°43.30' | ES | 15 |
| | 103 | CHAIN | 2022 | 39°43.60' | 70°37.40' | ES | 5 |
| <i>Benthomangelia antonia</i> | 2084 | ALBATROSS | 2359 | 40°16.83' | 67°05.25' | BT | 4 |
| | 62 | ATLANTIS | 2496 | 39°26.00' | 70°33.00' | ES | 1 |
| | 2096 | ALBATROSS | 2654 | 39°22.33' | 70°52.33' | BT | 3 |
| | 2221 | ALBATROSS | 2759 | 39°05.50' | 70°44.50' | BT | 9 |
| | 76 | CHAIN | 2862 | 39°35.30' | 67°57.50' | ES | 23 |
| | 72 | ATLANTIS | 2864 | 35°16.00' | 71°47.00' | ES | 12 |
| | 64 | ATLANTIS | 2886 | 35°46.00' | 70°06.00' | ES | 10 |
| | 2174 | ALBATROSS | 2915 | 35°15.00' | 72°03.00' | BT | 3 |
| | 2041 | ALBATROSS | 2941 | 39°22.53' | 65°25.00' | DST | 5 |
| | 2716 | ALBATROSS | 2983 | 35°29.50' | 70°57.00' | BT | 14 |
| | 2037 | ALBATROSS | 3166 | 35°53.00' | 69°23.50' | BT | 3 |
| | 2569 | ALBATROSS | 3259 | 39°26.00' | 65°03.50' | BT | 2 |
| | 340 | KNORR | 3310 | 35°16.00' | 70°21.55' | ES | 13 |
| | 2570 | ALBATROSS | 3316 | 39°54.00' | 67°05.50' | BT | 4 |
| | 2714 | ALBATROSS | 3335 | 35°22.00' | 70°17.50' | BT | 4 |
| | 2035 | ALBATROSS | 3715 | 35°30.50' | 69°05.42' | DST | 3 |
| | 95 | ATLANTIS | 3753 | 35°33.00' | 65°32.00' | ES | 2 |
| | 126 | ATLANTIS | 3806 | 39°37.25' | 66°45.50' | ES | 15 |
| | 77 | CHAIN | 3806 | 35°00.70' | 69°16.00' | ES | 7 |
| | 75 | CHAIN | 3825 | 35°00.50' | 69°15.70' | ES | 5 |
| | 55 | CHAIN | 3834 | 37°59.20' | 69°26.20' | ES | 5 |

the height plus width of the first post-larval whorl (Gould, 1969; Rex and Etter, 1990). Final size attained by adults, hereafter referred to as Adult Size, was measured as the maximum height plus width of the post-larval shell. Adult Size can not be standardized to a common development stage, because the species appear to have indeterminate growth. The distribution of Adult Size in a population reflects the recent history of recruitment and growth more than size as an adaptive property. To estimate the final size attained, we selected the largest two individuals (from any station) found in 250 m depth increments. These three measures of size (Protoconch Width, Whorl-1 Size, and Adult Size attained) were regressed against depth to analyze bathymetric clinal patterns.

RESULTS AND DISCUSSION

Relationships of size variables to depth are shown in figure 6. Regression lines are fitted only for significant relationships (see table 2 for regression equations and their

statistics). All significant regressions are positive, indicating an increase in size with depth. There is no indication that size decreases significantly with depth for any variable in either species. In *O. ovalis*, larval size increases with depth, but post-larval stages show no pattern. In contrast, *B. antonia* shows no relationship of larval size to depth, but both Whorl-1 Size and Adult Size do increase with depth.

These results largely confirm those reported by Rex and Etter (1998) for *B. antonia* and *O. ovalis*. The present study is more statistically accurate in that it includes larger sample sizes, broader depth coverage, and a much more continuous distribution of samples across the depth gradient. For Whorl-1 Size, both studies detected a strong positive increase with depth in *B. antonia* and no apparent trend in *O. ovalis*. For protoconch size, Rex and Etter (1998) reported a weakly significant ($p < 0.05$) increase with depth in *B. antonia*, and no relationship in *O. ovalis*. With more extensive sampling, the protoconch size-depth relationship becomes just insignificant ($p = 0.0589$) in *B. antonia*, and strongly significant in

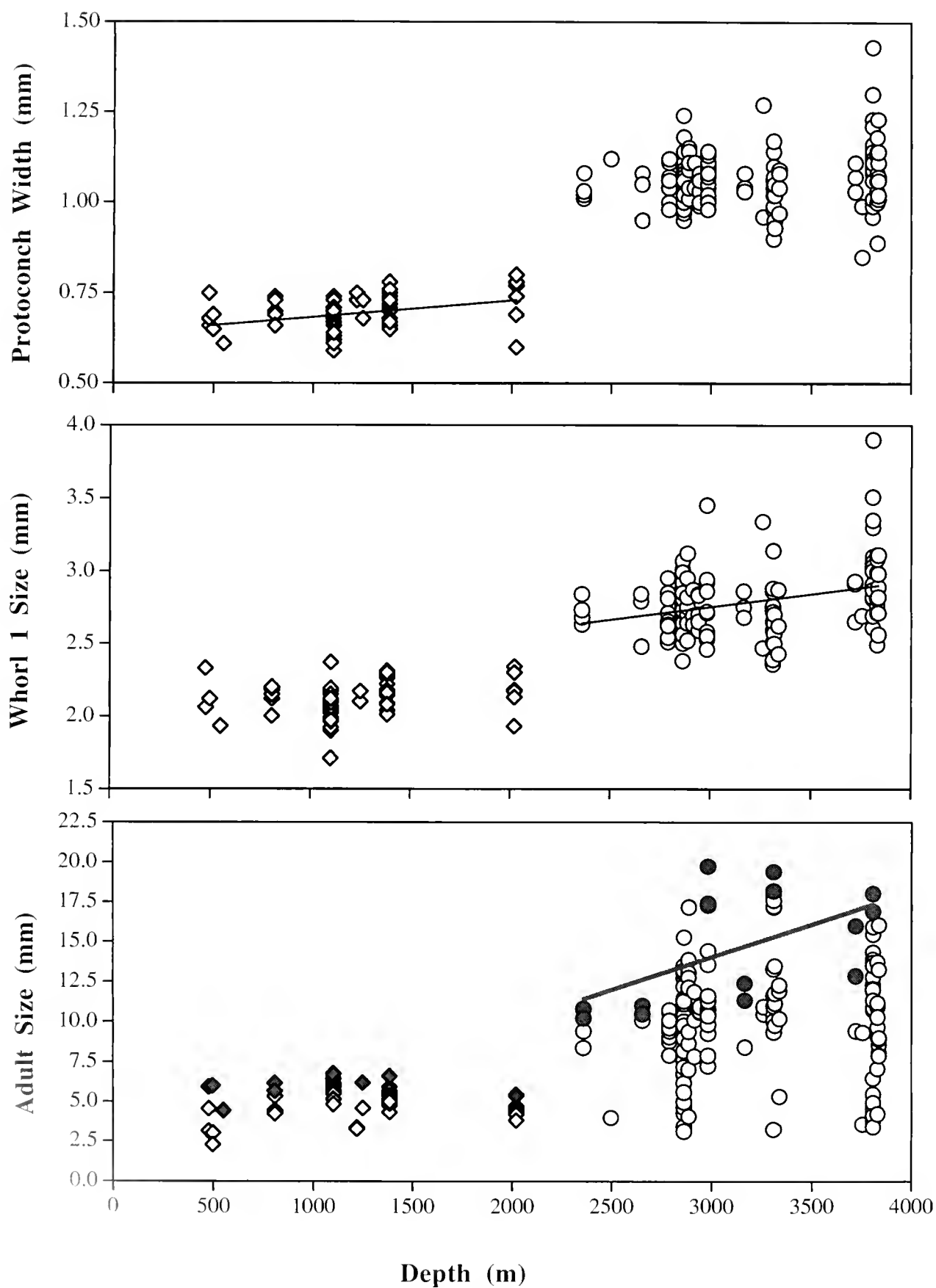


Table 2. Regression summary for relationships of size to depth in figure 6. For each regression, the number of individuals, regression equations, F-values, r^2 values, and the significance are given.

| Measurement | Species | Number of specimens | Regression equation | r^2 | F-value | Significance (p) |
|------------------|-------------------|---------------------|--------------------------|-------|---------|------------------|
| Protoconch width | <i>B. antonia</i> | 156 | $Y = 0.982 + 2.69E - 5x$ | 0.230 | 3.622 | 0.0589 |
| Protoconch width | <i>O. ovalis</i> | 69 | $Y = 0.639 + 4.54E - 5x$ | 0.147 | 11.507 | 0.0012 |
| Whorl 1 size | <i>B. antonia</i> | 135 | $Y = 2.219 + 1.78E - 4x$ | 0.106 | 15.850 | 0.0001 |
| Whorl 1 size | <i>O. ovalis</i> | 62 | $Y = 2.016 + 7.44E - 5x$ | 0.046 | 2.863 | 0.0958 |
| Adult size | <i>B. antonia</i> | 156 | $Y = 7.644 + 1.00E - 3x$ | 0.007 | 1.116 | 0.2925 |
| Adult size | <i>O. ovalis</i> | 69 | $Y = 5.171 - 2.88E - 5x$ | 0.000 | 0.010 | 0.9221 |
| Largest adult | <i>B. antonia</i> | 14 | $Y = 1.694 + 4.00E - 3x$ | 0.332 | 5.963 | 0.0310 |
| Largest adult | <i>O. ovalis</i> | 11 | $Y = 5.915 + 1.23E - 5x$ | 0.000 | 0.001 | 0.9772 |

O. ovalis. Rex and Etter (1998) did not estimate final adult size. As with studies of biodiversity (Rex *et al.*, 1997) and life-history characteristics (Stuart and Rex, 1994), the patterns in protoconch size that are revealed with better sampling demonstrate the importance of using large databases, and broad continuous depth gradients to establish biogeographic patterns in the deep sea. This is especially relevant for species like *B. antonia* that show high variability in shell architecture (figure 6).

It is interesting that *O. ovalis*, with non-planktotrophic development shows a size-depth cline only for larvae; whereas *B. antonia* with planktotrophic development exhibits no trend for larvae, but a significant positive cline for Whorl-1 Size that also persists at final size attained. For *B. antonia*, an explanation might be that larvae show no pattern because they migrate from numerous distant sites that may exert quite different selective regimes, and that selection for size at settlement along the depth gradients is not strong enough to overcome the mitigating effects of dispersal. In this context, it is interesting that larvae (and adults) of *B. antonia* show considerably more variation in size than those of *O. ovalis*, possibly reflecting multiple geographic origins for the former (figure 6). Selection for increased size with depth may be imposed largely during subsequent growth resulting in the positive size-depth cline seen in adult shells of *B. antonia*. The nature of the relevant depth-related selective gradient remains unknown. Rex and Etter (1998) suggested that the decrease in nutrient input with depth may select for larger size because of its metabolic and competitive advantages.

The opposite pattern observed in *O. ovalis* is difficult to interpret in a consistent way. Larger size at hatching may confer advantages of lower vulnerability to predators, greater locomotion to forage, a greater range of food, and more ability to withstand starvation (Spight, 1976). However, the absence of a size cline at adult stag-

es is puzzling. In general, the results do indicate that different life stages can respond differently and independently to environmental changes associated with depth. Since the species live at different depths, a geographically controlled comparison is not possible. Also, because we are analyzing just two species, the results may represent idiosyncratic effects that are phenotypic plastic responses or phylogenetic constraints, rather than general patterns that are related to selective gradients and developmental modes.

In summary, the upper bathyal *O. ovalis* shows a significant positive size-depth cline for larvae, but not adults. The lower bathyal *B. antonia* reveals no depth-related pattern for larval shells, but a significant increase in size with depth for adults. The exact causes of these opposing trends are necessarily speculative; but, the results do suggest that larvae and adults may respond differently to selective gradients in species with contrasting modes of development in the deep sea as they appear to do in coastal mollusks (Pechenik, 1999; Pechenik *et al.*, 1996). The increase in size with depth generally supports earlier studies on geographic variation in deep-sea gastropods (Rex and Etter, 1990, 1998; Rex *et al.*, 1999). However, detailed analyses of individual species highlight the need for large databases and good sampling coverage throughout species' bathymetric ranges to accurately assess biogeographic patterns in deep-sea organisms.

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Figure 6. Relationships of Protoconch Width (top), Whorl-1 Size (middle), and Adult Size (bottom) to depth in populations of *Ocnopota ovalis* (diamonds) and *Benthomangelia antonia* (circles) collected in the deep sea of the western North Atlantic. The solid symbols in the Adult Size graph indicate the largest two individuals found in each 250 m interval. Lines indicate significant regressions. See table 2 for regression statistics.

measured and analyzed here. This research was supported by the National Science Foundation Grant OCE-9301687 to MAR, and by the University of Massachusetts.

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Four new genera for northeastern Pacific gastropods

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ABSTRACT

Four new genera for northeastern Pacific Gastropoda are proposed: Velutinidae: *Torellivelutina*, type species "*Torellia*" *ammonia* Dall, 1919; Eulimidae: *Subniso*, type species "*Chemnitzia*" *rangi* de Folin, 1867; Turridae, Clathrellinae: *Retidrillia*, type species "*Suavodrillia*" *willetti* Dall, 1919; Mangeliinae: *Perimangelia*, type species "*Mangelia*" *interfossa* Carpenter, 1864.

Additional key words: Gastropoda, Eulimidae, Turridae, Velutinidae.

INTRODUCTION

This is the third in a series of papers in which new genera for northeastern Pacific gastropods are introduced (see McLean, 1995a, b). I had previously indicated (McLean, 1995a) that a checklist of the northeastern Pacific gastropods was in preparation; however, as indicated in McLean (1996: 2), I am preparing a more complete work rather than a checklist. Taxa described here are to be used in an illustrated revision of all shelled gastropods of the northeastern Pacific, ranging from Arctic Alaska and the Aleutian Islands to central Baja California, Mexico. Description of these genera in advance of the book allows for a more detailed treatment than will be possible in the larger effort. Further papers in this series will describe genera in which the type species or other included species are new.

To distinguish original combinations for type species of the new genera I am here using the convention of placing all citations of original genera within quotation marks. Illustrations are provided here for type species of each new genus.

Although monotypic genera are not encouraged in phylogenetic classifications, I do not refrain from introducing a few such genera where necessary, allowing that additional living or fossil species may yet be discovered that would render those genera no longer monotypic.

Museum acronyms are: LACM, Natural History Museum of Los Angeles County; USNM, National Museum of Natural History, Washington.

SYSTEMATICS

Family Velutinidae Gray, 1840

Genus *Torellivelutina* new genus

Type species: "*Torellia*" *ammonia* Dall, 1919 (Figure 1). The shriveled holotype from offshore depths at the Aleutian Islands, Alaska, was illustrated by Warén (1989: 16, fig. 11f). A more recently collected, preserved specimen from the Aleutian Islands is illustrated here.

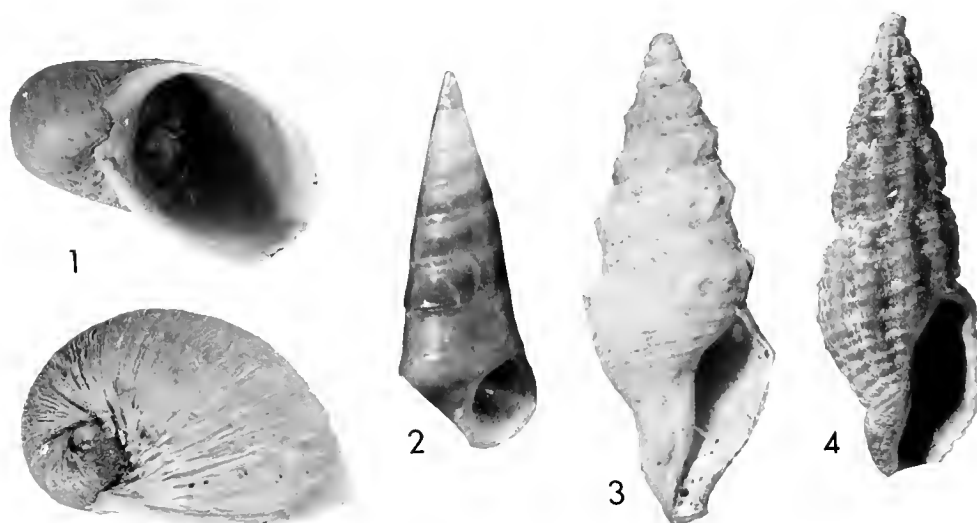
Included species: The genus is monotypic.

Diagnosis: Shell large (to 30 mm diameter), apical whorl depressed, profile nearly planispiral, of two rapidly inflated whorls, calcareous layer lacking in large specimens except for that which borders the apertural lip; shell consisting of chitinous periostracum after attaining 3 mm diameter; protoconch with spiral sculpture (according to original description of Dall); suture deep, umbilicus broad; mature surface composed of thick, chitinous, colabral axial lamellae.

Remarks: Warén (1989: 16) examined the type species for purposes of comparison with his then described new genus and species *Pseudotorellia fragilis* from Iceland. He illustrated the radula of "*Torellia*" *ammonia* (*op. cit.*, fig. 11c), which he found to agree with that of other velutinid radulae, and reported that the operculum and other trichotropine features are lacking. Although Warén removed "*T.*" *ammonia* from the trichotropid genus *Torellia*, and transferred it to the Velutinidae, he did not assign it to a genus. *Torellivelutina* is therefore here proposed for "*T.*" *ammonia*. It differs from *Pseudotorellia* in not having a solid calcified shell with spiral sculpture and not having the large, projecting protoconch of *Pseudotorellia*.

Because the calcareous layer is lacking, fresh specimens of *Torellivelutina ammonia* should be retained in fluid preservative and should not be dried, which results in the shrinkage and buckling of the thick periostracal layer.

Etymology: The name is a compound of the trichotropid genus *Torellia* and the velutinid genus *Velutina*,



Figures 1–4. Type species of new genera. **1.** *Torellivelutina ammonia* (Dall, 1919), apertural and spire views. LACM 152281, Kanaga Pass, between Kanaga Island and Tanaga Island, Andreanof Islands, Aleutian Islands, Alaska, 61 m. Maximum diameter 30 mm. **2.** *Subniso rangi* (de Folin, 1867). LACM 1972-38.7, Punta Penca, N of Bahia Potrero, Guanacaste Prov., Costa Rica, 10 m. Length 3.2 mm. **3.** *Retidrillia willetti* (Dall, 1919). USNM 216409, lectotype. Forrester Island, southeast Alaska, dredged. Length 11.5 mm. **4.** *Perimangelia interfossa* (Carpenter, 1864). LACM 1959-13.42, Granite Creek, Monterey County, California, 10 m. Length 8.5 mm.

to emphasize that it represents a velutinid with the superficial aspect of the trichotropid genus *Torrellia*.

Family Eulimidae Philippi, 1853
Genus *Subniso* new genus

Type species: “*Chemnitzia*” *rangi* de Folin, 1867 (Figure 2). Type locality: Perlas Islands, Panama. Warén (1992: 183) could not locate type material, but the species was well figured by de Folin and subsequently by Warén (1992, figs. 17, 20–22, 25–27, 30, 31), so there is little doubt as to its identity. The species occurs from southern Baja California, Mexico, to Ecuador.

Included species: Two species, the type species and “*Niso*” *hipolitensis* Bartsch, 1917, for which the holotype from Punta San Hipolito, Baja California, Mexico, was illustrated by Emerson (1965, fig. 9) and Warén (1992: figs. 19, 23, 24). Both species have previously been placed in *Niso* Risso, 1826, by Emerson (1965) and Warén (1992).

Diagnosis: Shell small (length to 4 mm), slender (length to breadth ratio 2.5–2.9), non-umbilicate, basal angulation pronounced, coloration brown, without color pattern.

Remarks: The two species of *Subniso* are unlike other species of *Niso* in size, profile, and color. The two species are small, non-umbilicate, and have a basal angulation (strongly projecting in *Subniso rangi*) and a uniform brown coloration. Warén (1992: 185) remarked: “Both *Niso hipolitensis* and *N. rangi* are unusual among the species of *Niso* in their small size, 3–4 mm shell height,

whereas most species of the genus have a shell that is 10–30 mm high, occasionally even higher.” Additionally, I point out that *Niso* species are usually broadly umbilicate, except for the large *N. attilloi* (Hertz and Hertz, 1982), usually not angulate at the base, and have color patterns that may be banded or variegated. Taken together, these differences are sufficient to justify generic recognition of *Subniso*.

Warén (1992: 183) noted that a starfish host is known for one Indo-Pacific species of *Niso*, but nothing is known of the host echinoderm for the two species of *Subniso*.

Etymology: The generic name combines the generic name *Niso*, with the prefix *sub-*, to emphasize the small size, compared to *Niso*.

Family Turridae Swainson, 1840
Subfamily Clathurellinae H. and A. Adams, 1858
Genus *Retidrillia* new genus

Type species: “*Suavodrillia*” *willetti* Dall, 1919 (Figure 3). Type locality: Forrester Island, Southeast Alaska. Until now the species has been unfigured (it was not illustrated by Kosuge, 1972). The here selected lectotype (Figure 7) is the largest (11.3 mm) of seven original syntype specimens in the type lot. The radular tooth of the type species was figured by McLean (1971, fig. 114) (from LACM 66-66, Graham Island, Queen Charlotte Islands, British Columbia). A specimen from the Rae Baxter collection in the LACM extends the distribution to Akutan, Aleutian Islands (LACM 83-345, 263 m depth).

Included species: At least three species, the type species and two species from the northeastern Atlantic discussed and illustrated by Bouchet and Warén (1980: 32) in the genus *Drilliola* Locard, 1897: "*D.*" *pruina* (Watson, 1881), and "*D.*" *megalaeme* (Sykes, 1906).

Diagnosis: Shell profile with concave shoulder and projecting peripheral carination below which base is rounded and has strong spiral sculpture. Anal sinus on concave shoulder, deep and broad. Axial sculpture expressed as nodes, strongest at peripheral carination, more faintly expressed on strong spiral cords of base. Peripheral carination of early whorls at midwhorl. Protoconch paucispiral, with early development of peripheral carination. Radular tooth long, harpoon-like, with broad base.

Remarks: The type species was described in the genus *Suavodrillia* Dall, 1918 (type species: "*Drillia*" *kennicotti* Dall, 1871), with which it shares the long harpoon-like radular tooth. Dall (1921: 69) indicated doubt that "*S.*" *willetti* was congeneric by placing a question mark preceding the genus. Differences are that *Retidrillia willetti* and the two additional species here assigned to the genus are half the size of *S. kennicotti*, and have sculpture that is axial and spiral, rather than strictly spiral as in *Suavodrillia*. The newly restricted *Suavodrillia* is monotypic for *S. kennicotti*, a species broadly distributed in the north Pacific from Hokkaido, Japan, the Kurile and Aleutian Islands, and the Gulf of Alaska to Southeastern Alaska.

Bouchet and Warén (1980: 32) retained "a wide variety of species" in *Drilliola*, including those that "look rather different but have a similar radula and operculum." They elected "to keep them in *Drilliola* rather than placing them in any of the perhaps more similar, but anatomically unknown genera listed by Powell (1966) in different subfamilies." Species typical of *Drilliola* are more slender than those of *Retidrillia* and do not have the broad, excavated shoulder. The proposal of *Retidrillia* thus provides a genus with a type species having known radular characters for the two species cited by Bouchet and Warén (1980).

On shell characters, *Retidrillia* resembles species assigned to *Plicisyrinx* Sysoev and Kantor, 1986, in which the radular tooth is of the modified wishbone type, indicative of the less derived turrid subfamily Cochlespirinae.

Etymology: The name is a compound of *reti*-, meaning net, with reference to the axial and spiral sculpture, and *Drillia* Gray, 1838, one of the earliest named of turrid genera.

Subfamily Mangeliinae Fischer, 1883

Genus *Perimangelia* new genus

Type species: "*Mangelia*" *interfossa* Carpenter, 1864 (Figure 4). Syntypes were figured by Palmer (1958, pl. 27, figs. 5, 6). Also figured by McLean (1969; 1978, fig.

30-4). Synonym: "*Mangelia*" *interlirata* Stearns, 1872. The species occurs from Clallam County, Washington, to Isla San Geronimo, Baja California, Mexico, based on specimens in the LACM collection.

Included species: Two species, the type species and the less familiar "*Mangelia*" *nitens* Carpenter, 1864 (syn-type figured by Palmer, 1958, pl. 28, fig. 1). It ranges from Sonoma County, California, to Ensenada, Baja California.

Diagnosis: Shell relatively small and slender with dominant axial sculpture, crossed by narrow spiral cords of lesser strength. Protoconch of 1.5 whorls, strongly projecting, smooth at first, developing fine spiral sculpture after first half whorl, followed by weaker axials (axials more numerous than that of mature sculpture), changing imperceptibly to adult sculpture.

Remarks: Earlier (McLean, 1978: 74), I placed the type species of the new genus ("*Mangelia*" *interfossa*) along with "*Daphnella*" *fusciligata* Dall, 1871 in *Clathromangelia* Monterosato, 1884. I now consider *Clathromangelia* (type species "*Pleurotoma*" *granum* Philippi, 1844; see Powell, 1966: 106) to be appropriate for two species in southern California: "*Daphnella*" *fusciligata* and "*Mangilia* (*Clathromangelia*)" *rhyssa* Dall, 1919. These two species have coarse clathrate sculpture and relatively low, paucispiral protoconchs.

Perimangelia differs from the two species of *Clathromangelia* in having numerous, narrow spiral cords overriding the dominant axial ribs, rather than having coarsely clathrate sculpture with nodes at intersections. Protoconchs differ: the paucispiral protoconch of the two species of *Perimangelia* is strongly projecting, whereas the paucispiral protoconch of the two species of *Clathromangelia* is much lower.

Etymology: The name combines the prefix *peri*-(near) with *Mangelia* Risso, 1826, one of the oldest genera in the subfamily Mangeliinae.

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Obscuranella papyrodes, a new genus and species of abyssal tonnoidean gastropod from Antarctica

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ABSTRACT

The new genus *Obscuranella* and *O. papyrodes*, its type species, are described from the abyssal plain off the Ross Sea, Antarctica. *Obscuranella* is included in the primarily tropical, shallow water superfamily Tonnoidea because it has a taenioglossan radula, extensible proboscis, large salivary glands composed of anterior and posterior lobes, salivary ducts that pass through the nerve ring, and an undifferentiated oesophageal gland. This taxon is precluded from the families Laubierinidae, Pisanianuridae, and Tonniidae because it lacks a monopectinate osphradium, paired proboscis retractor muscles passing through the nerve ring, buccal glands, and rachidian teeth with lateral basal denticles. *Obscuranella* is assigned to the family Ranellidae primarily on the basis of shell, radular, and opercular morphology. This is the first report of the Tonnoidea in Antarctic waters, and the first record of Ranellidae from abyssal depths.

Additional key words: Caenogastropoda, Ranellidae, anatomy, systematics.

INTRODUCTION

In the course of examining Antarctic Buccinoidea sampled under the auspices of the United States Antarctic Program (USAP) and housed in the National Museum of Natural History, Smithsonian Institution, we encountered five lots of gastropods with large bucciniform shells that had tentatively been attributed to the buccinoidean genus *Bathydromus* Thiele, 1912, by Dell (1990:198–199). Dell identified four of these lots as *Bathydromus obtectus* Thiele, 1912, but considered the fifth lot, consisting of a single specimen, to represent an undescribed species of *Bathydromus*. Dissections of preserved material clearly demonstrate that these gastropods are not referable to Buccinoidea, nor even to Neogastropoda, but rather represent an unnamed genus and species of the superfamily Tonnoidea. This is the first report of this superfamily in the Antarctic malacofauna, and one of very few records of the Tonnoidea from the abyssal zone. The family Ranellidae, to which this genus is assigned,

has not previously been reported from the Antarctic or from abyssal depths.

In this paper, we provide descriptions of this new genus and new species, and infer its taxonomic position within the Tonnoidea by comparing its anatomy, radula and operculum with published anatomical reports (e.g. Weber, 1927; Houbbrick and Fretter, 1969; Day, 1969; Beu, 1981; Hughes and Hughes, 1981). Warén and Bouchet (1990), Riedel (1995), and Beu (1998) each provide useful, if not entirely congruent, syntheses of tonnoidean families, and include anatomical descriptions as well as numerous illustrations of radulae, opercula and protoconchs. Abbreviations used in the descriptions of morphometric characters are explained in Table 1.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Superfamily Tonnoidea Suter, 1913
Family Ranellidae Gray, 1854

Genus *Obscuranella* new genus

Type species: *Obscuranella papyrodes* new species

Diagnosis: Protoconch unknown. Teleoconch large, pyriform, thin, with large aperture, single, rounded, unthickened terminal varix adjacent to thin, flared outer lip in adult specimens. Shell sculpture limited to fine, widely spaced, spiral cords. Operculum very small, sharply tapering anteriorly, with anterior terminal nucleus. Proboscis wall extremely thick, paired proboscis retractor muscles absent. Rachidian teeth lacking lateral basal denticles. Salivary glands large, differentiated. Osphradium bipectinate.

Etymology: *Obscurus* (L.)—obscure, unclear + *Ranella*—genus of Ranellidae.

Obscuranella papyrodes new species
(Figures 1–36, Table 1)

Bathydromus obtectus Thiele, 1912—Dell, 1990:198–199, figs. 299–300.

Table 1. *Obscuranella papyrodes*, new species. Measurements of shell characters. Linear measurements in mm.

| Character | Holotype | Paratype 1 | Paratype 3 | USNM 901317 | USNM 870610 | USNM 870610 |
|---|----------|------------|------------|----------------|----------------|----------------|
| Shell Length (SL) | 63+ | 58+ | 33+ | 57.0 | 43.6+ | 33.2+ |
| Last Whorl Length (LWL) | 55.2 | 51.8 | 28.5 | 47.3 | 38.5 | 30.4 |
| Aperture Length (AL) | 45.1 | 43.3 | 23.0 | 38.4 | 31.5 | 25.5 |
| Shell Width (SW) | 40.8 | 41.5 | 19+ | 34.1 | 24+ | 20.2+ |
| Number of spiral cords on last whorl | 14 | 12 | 14 | 5 | 14 | 13 |
| Number of spiral cords on penultimate whorl | 6 | 7 | 7 | 2 | 5 | 3 |

Bathynomus sp.—Dell, 1990:199.

Description: Shell large (exceeding 63 mm), very thin, fragile, ovate-pyriform. Protoconch and upper whorls missing in all type material. Preserved portions of teleoconch of 2½ rapidly expanding, evenly rounded whorls. Shoulder rounded, indistinct. Suture adpressed, shallow. Axial sculpture limited to fine, straight, weakly prosocline growth lines. Adult specimens with a single, weak, hollow varix adjacent to thin, flared outer lip (figures 2, 7, arrow). Spiral sculpture of sharp, narrow, evenly spaced cords (14 on last whorl, 6 on penultimate whorl), with much weaker sinuous threads (22–30) of varying width between adjacent cords. Aperture large [~ 0.7 shell length (SL)], broadly ovate, deflected from shell axis by 9–11°. Outer lip thin, evenly rounded in upper part and concave at transition to siphonal canal, weakly reflected. Inner lip consisting of long, convex, medially indented parietal region and short, smooth, axial columella with strong, long siphonal fold that crosses coiling axis of shell. Siphonal canal short, broad, weakly recurved dorsally. Callus of thin, white, porcellaneous glaze overlying parietal region, adapical portion of broad, nearly axial siphonal fasciole. Shell color pale olive-tan, confined to outermost shell layer. Aperture white. Periostracum very thin, yellowish brown, with densely spaced axial lamellae, occasional short hairs at intersection of lamellae with spiral cords. Operculum (figures 4, 5) very small (0.16 AL), vestigial, dark yellow, subtriangular, with straight sides, terminal nucleus. Dorsal surface with numerous, closely spaced growth lines. Ventral surface with thin, glazed lateral margins. Operculum attached over most of its surface.

Shell ultrastructure (Figure 23): Shell thin (101 μm), composed of three layers. Outermost layer (figure 23, ca) thinnest (4 μm), composed of columnar crystals. Middle layer (figure 23, cel) thickest (79 μm), composed of collaterally oriented cross-lamellar crystals. Inner layer (figure 23, rel) thin (18 μm), composed of cross-lamellar

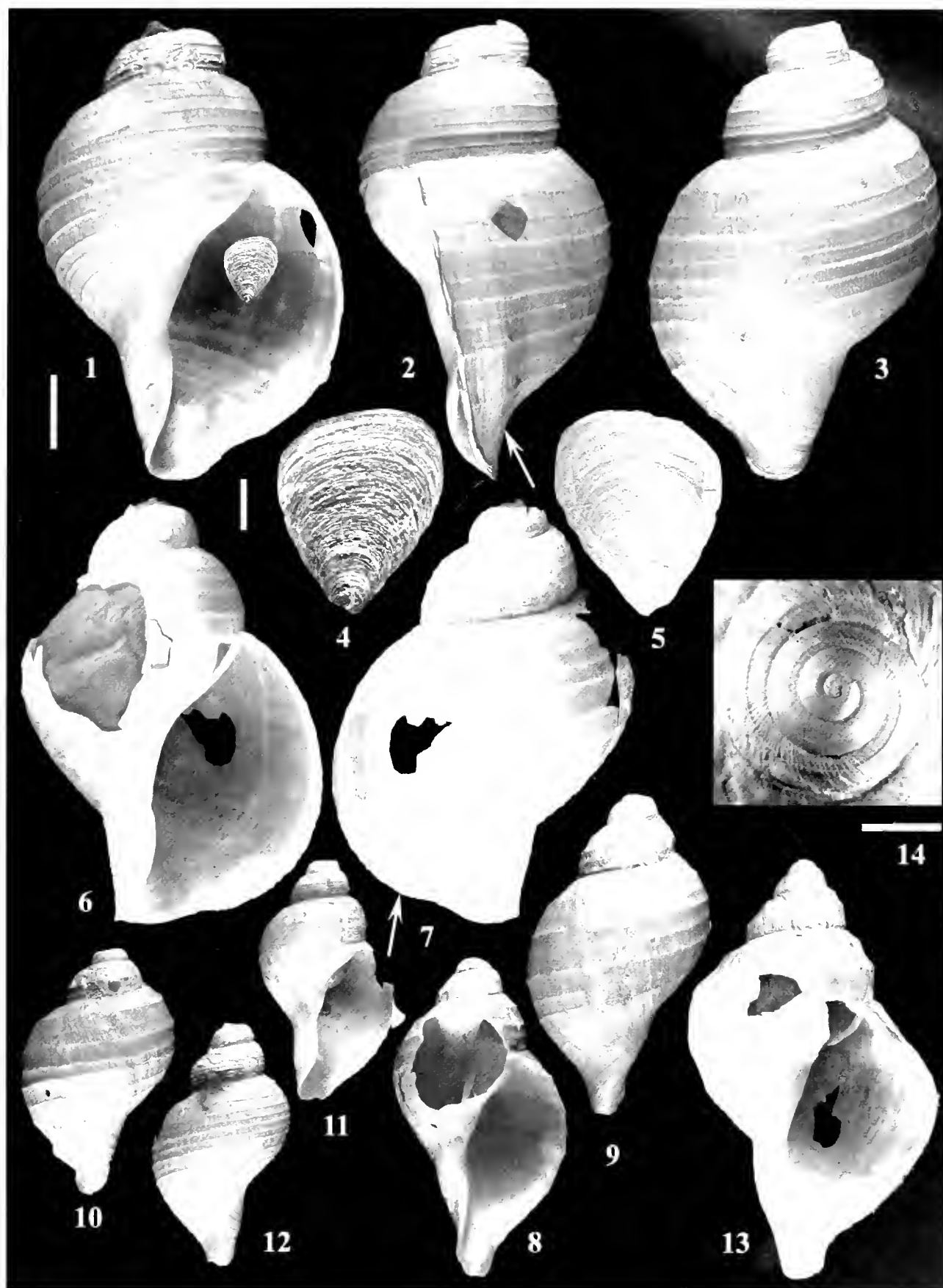
crystals oriented perpendicular to growing edge of the shell.

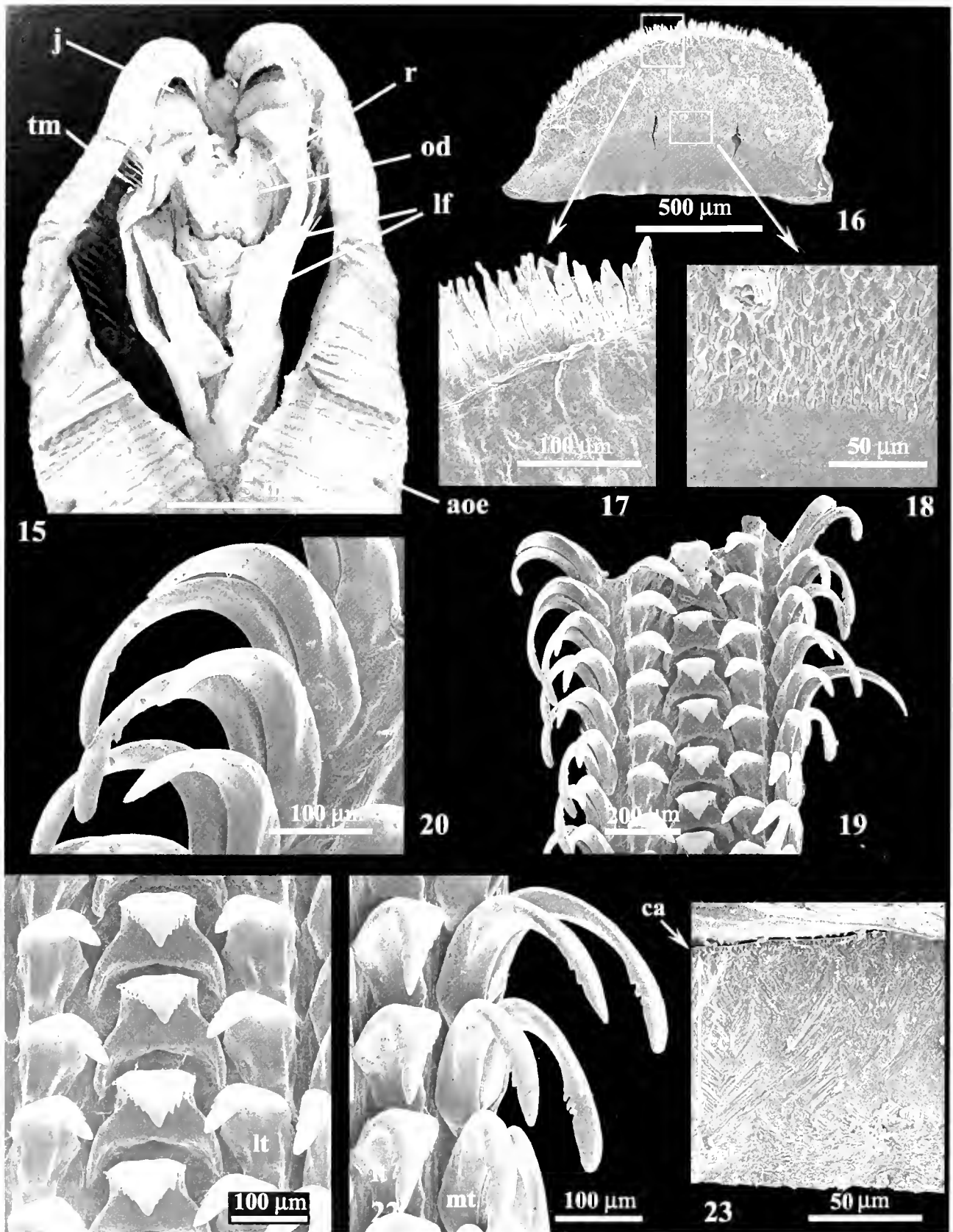
Anatomy (Paratype 1, ♀): Soft tissues comprising approximately 3½ whorls. Mantle cavity spans just under ½ whorl, nephridium (figures 24, 25, 27, n) about ¼ whorl, digestive gland (figures 24, 25, dg) 2½ whorls. Mantle edge (figures 24, 25, 27, me) thickened, smooth, completely covers head. Columellar muscle (figure 25, cm) thick, broad, spanning slightly more than one whorl, attached to shell at rear of nephridium. Foot short in contracted state (Length/Width ≈ 1.0), with conspicuous propodium. Body color uniform reddish-tan, without pattern in alcohol preserved specimens. Head (figure 26) very large, as wide as foot, with broad, blunt, tapering tentacles (figure 26, tn) with black eyes at their bases. Operculum about 4 mm long (0.09 AL), otherwise similar to that of holotype. Paratype 1 (and all other preserved specimens) with proboscis protruded through very wide rhynchostome (figure 26).

Mantle cavity (Figure 27): Mantle cavity as deep as broad ($\sim ½$ whorl). Siphon (figures 24, 25, 27, s) broad, muscular, very short, extending slightly beyond mantle edge (figures 24–27, me). Osphradium (figures 24–27, os) situated along central half of ctenidium, bipectinate, nearly symmetrical, slightly narrower on left side than right. Ctenidium (figures 24–27, ct) long, spanning nearly entire mantle length, formed of tall triangular lamellae, nearly twice as high as broad. Hypobranchial gland (figure 27, hg) poorly developed, lacking distinct folds. Rectum (figure 27, re) runs along inner surface of pallial oviduct, narrow, terminating in simple anus (figure 27, a) behind thickened mantle edge.

Alimentary system (Figures 15, 19–22, 24, 32–35): Everted proboscis (figures 24–26, pr) ~ 30 mm long (0.7 AL), unpigmented, with folded walls indicating potential for further extension. Proboscis wall very thick, $\sim 60\%$

Figures 1–14. *Obscuranella papyrodes* new species. 1. Apertural, 2. right lateral, and 3. dorsal views of the holotype, USNM 898683. 4. External and 5. internal views of the operculum of the holotype (internal view coated with Ammonium chloride to emphasize sculpture). 6. Apertural and 7. dorsal views of paratype 1, USNM 896131. 8. Apertural and 9. dorsal views of the larger shell, 10. dorsal view of smaller shell, USNM 870610. 11. Apertural and 12. dorsal views of paratype 3, USNM 886105. 13. Apertural view and 14. apical view of early whorls of USNM 901317. Scale bar = 1 cm for all shells; Scale bar = 2 mm for operculum; Scale bar = 5 mm for protoconch.





of proboscis radius, composed of 3 layers of muscles. Innermost layer of circular muscles (figure 32, cm), middle layer thickest (2/3 of proboscis wall), of longitudinal muscles (figure 32, lm), outer layer of circular muscle. Buccal mass (figure 33, bm) small, attached to proboscis walls by numerous, thin tensor muscles (figures 15, 32, 33, tm), as is the anterior oesophagus (figures 15, 32, aoe). Retractor muscles passing through nerve ring and joining buccal mass and columellar muscle absent. Mouth (figure 32, mo) a narrow, vertical slit. Buccal tube (figure 33, bt) short, leading to cuticle-lined buccal cavity with ventral pair of semicircular jaws (figure 33, j). Jaws (figures 16–18) dark brown, pappilate along outer edge (figure 17). Inner surface of jaw composed of small, closely spaced platelets that produce “cobble” surface distally (figure 18), smooth proximally (figure 16). Odontophore (figure 15, od) small, oval, lining bottom of the buccal cavity. Walls of buccal cavity very thick. Proboscis nerves (figure 32, pn) paired, very thick, running from cerebro-pleural ganglia along proboscis length, innervating buccal mass and anterior part of proboscis. Anterior esophagus divided into dorsal and ventral channels by prominent longitudinal folds (figures 15, 34, 35, lf) that extend from the buccal cavity to the posterior edge of esophageal gland. The right fold overlaps the left (figure 34). Radular ribbon (figure 19) short (5.8 mm, 0.13 AL), nearly twice as long as cartilages, narrow (~ 580 μ m, 0.013 AL), consisting of 45 rows of teeth, posteriormost 4 rows nascent. Rachidian tooth (figure 21, rt) with large, broad median cusp, flanked by 5–9 denticles per side. Base broad, strongly concave posteriorly, lacking cusps along tooth base. Lateral teeth (figures 21, 22, lt) narrow, with long, thin, cusp flanked by 3–4 denticles on inner edge, 4–6 denticles on outer edge. Two long, recurved, distally flattened marginal teeth (figures 20; 22, mt) per side, outer tooth longer than inner. Inner distal edges serrated with 2–7 cusps. Salivary glands large, irregularly shaped, completely covering the esophageal gland (figure 32, oeg). Right salivary gland more elongated, slightly larger than left. Each gland consists of two lobes. Posterior lobe (figure 32, plsg) massive, composed of curved radially oriented blind tubules. Anterior lobe (figure 32, als) smaller, acinous, ventral. Salivary ducts (figures 32–34, sd) thick, extending from posterior lobes, becoming attached to oesophagus walls before passing through nerve ring. We were not able to identify connections between the salivary ducts and the anterior lobes of the salivary glands, as reported for *Cymatium intermedium* (Pease, 1869) by Andrews *et al.* (1999). Salivary glands

attached to oesophagus by thin muscular and connective tissue fibers and innervated by several nerve branches. Esophageal gland formed of deeply glandular dorso-ventral folds, small relative to salivary glands, of the same color as surrounding tissues and esophagus. Stomach large, U-shaped, similar to that of *Cymatium nicobari-cum* (Houbick and Fretter, 1969) in external morphology, too poorly preserved to reveal details of internal morphology, except that the ducts of the digestive gland are paired, closely spaced, and situated in the middle region of the stomach. Posterior duct twice the diameter of anterior duct. After leaving stomach intestine curves dorsally, passing under then along posterior edge of nephridium towards rear of mantle cavity (figures 24, 25, in).

Female reproductive system (Figures 25, 27–30):

The only specimen dissected (Paratype 1) was a mature female. Pallial oviduct consists of small albumen gland (figure 25, ag) along outer wall of nephridium, large capsule gland (figures 25, 27, cg) lining right wall of pallial cavity. Lumen of capsule gland small anteriorly (figure 29), broad posteriorly (figure 28), at juncture to albumen gland. No seminal receptacles were identified, possibly due to poor fixation. Bursa copulatrix (figures 27, 29, 30, bc) large, long, spanning more than half length of capsule gland. Pallial oviduct opens (figures 27, 29, go) by long, narrow slit at midlength.

Male reproductive system (Figure 31): The reproductive system of a male specimen lacking shell (paratype 2) was examined. Testes occupy upper half of whorls of visceral mass above posterior border of stomach, giving rise to seminal duct. Seminal duct forms large, convoluted seminal vesicle before entering mantle cavity. Duct descends to floor of mantle cavity at midlength, opening to form groove with thickened, obviously glandular walls leading to penis base. Penis (figure 31, p) broad, dorsoventrally flattened, with seminal groove (figure 31, sgr) running along inner edge, around the bluntly rounded distal edge, halfway down the outer edge, terminating in a very small, inconspicuous papilla (figure 31, pap).

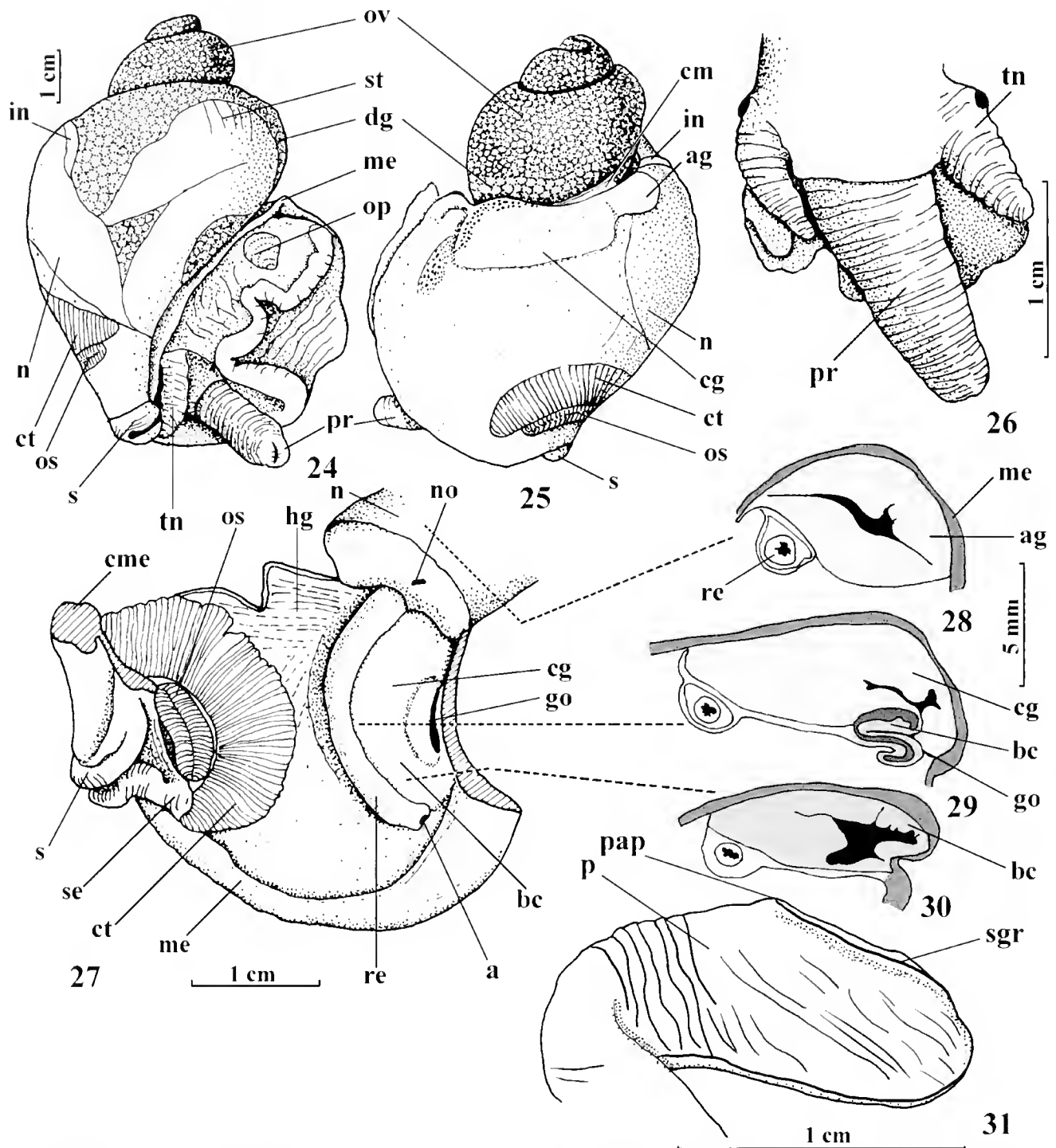
Type locality: Victoria Land, Balleny Islands, Sturge Island, R/V *Eltanin*, st. 1949, 66°52'S, 164°32'E, in 2507–2525 m, 5 February 1967.

Type material: Holotype, USNM 898683 (figures 1–5, shell and operculum only, soft parts not present), from the type locality; paratype 1, USNM 896131 (figures 6–

←

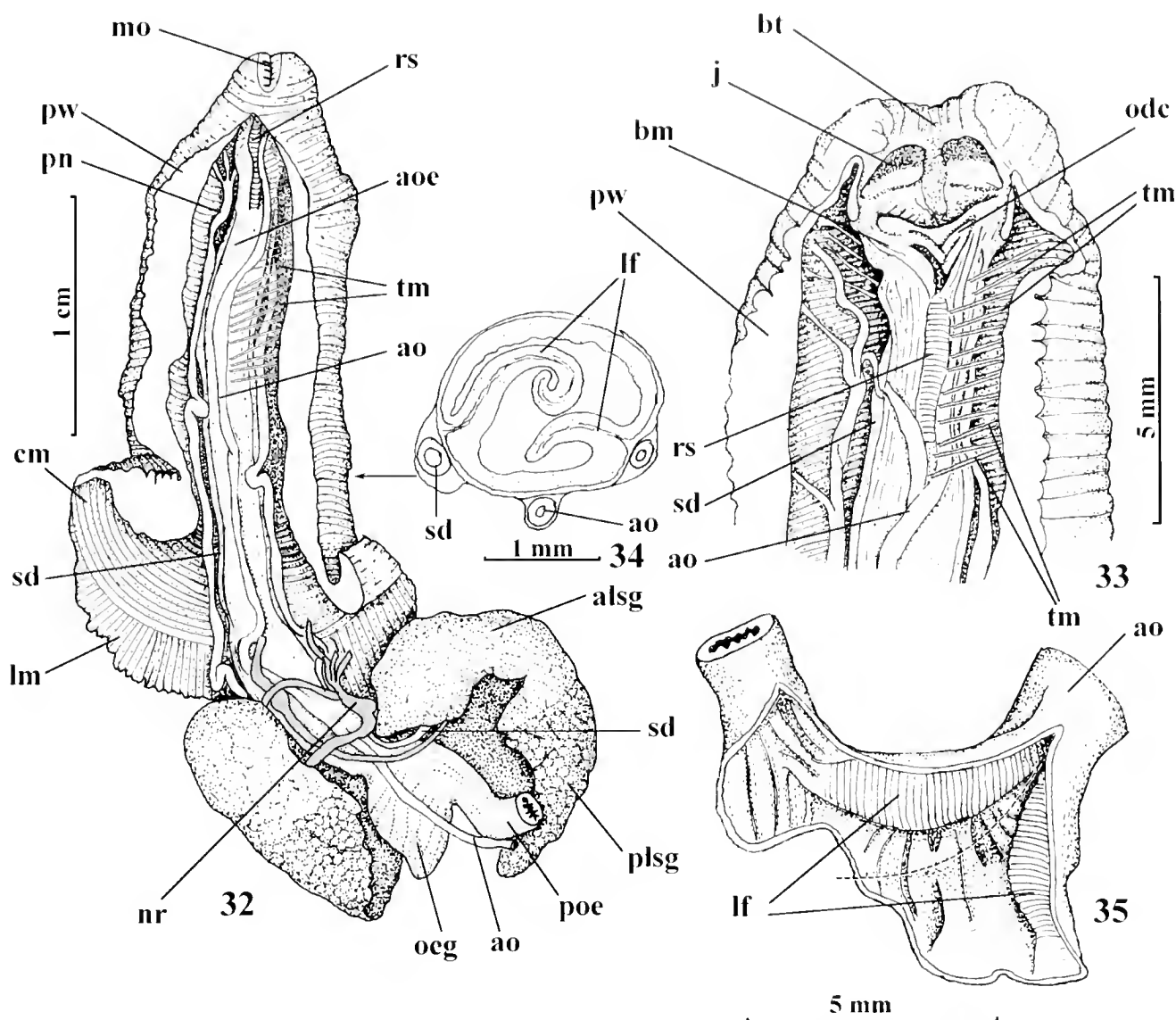
Figures 15–23. *Obscuranella papyrodes* new species. Paratype 1, USNM 896131. **15.** Distal end of the proboscis opened dorsally. **16–18.** Left jaw. **16.** Entire inner surface of jaw. **17.** Enlarged section of the upper edge. **18.** Enlarged section of the surface in the middle part of the jaw. **19–22.** Radula. **19.** View spanning width of radular ribbon. **20.** Left marginal teeth. **21.** Rachidian and lateral teeth. **22.** Right lateral and marginal teeth, tilted to 30°. **23.** Ultrastructure of the shell (Paratype 3, USNM 886105).

aoe, anterior oesophagus; lf, lateral folds; od, odontophore; ca, columnar shell layer; ecl, comarginal crossed lamellar shell layer; j, jaw; lt, lateral teeth; mt, marginal teeth; r, radula; rcl, radial crossed lamellar shell layer; rt, rachidian tooth; tm, tensor muscles.



Figures 24–31. *Obscuranella papyrodes* new species. Paratype 1, USNM 896131. **24.** Ventral and **25.** dorsal views of animal removed from the shell. **26.** Antero-dorsal view of the head. **27.** Mantle complex, opened from left side and reflected. **28–30.** Schematic sections through the pallial gonoduct. **31.** Penis (Paratype 2).

a, anus; ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; dg, digestive gland; go, genital opening; hg, hypobranchial gland; in, intestine; me, mantle edge; n, nephridium; no, nephridial opening; op, operculum; os, osphradium; ov, ovary; p, penis; pap, papilla; pr, proboscis; re, rectum; s, siphon; se, siphonal edge; sgr, seminal groove; st, stomach; tn, cephalic tentacle.



Figures 32–35. *Obscuranella papyrodes* new species. Anterior alimentary system, Paratype 1, USNM 896131. **32.** Proboscis (opened ventrally) and organs of cephalic haemocoele. **33.** Anterior part of the proboscis, opened ventrally. **34.** Transverse section through anterior oesophagus, viewed from anterior. **35.** Esophageal gland, opened dorsally. Dashed line indicates ventral midline.

alsg, anterior lobe of the salivary gland; ao, anterior aorta; aoe, anterior oesophagus; bm, buccal mass; bt, buccal tube; cm, circular muscle layer of the proboscis wall; j, jaw; lf, longitudinal fold of anterior oesophagus; lm, longitudinal muscle layer of the proboscis wall; mo, mouth opening; nr, nerve ring; odc, odontophore cartilages; oeg, oesophageal gland; plsg, posterior lobe of the salivary gland; pn, proboscis nerve; poe, posterior oesophagus; pw, proboscis wall; rs, radular sack; sd, salivary duct; tm, tensor muscles.

7, ♀ specimen, anatomical descriptions based on this specimen), paratype 2, USNM 896139 (♂ specimen, shell not present, male reproductive system based on this specimen), both from south of Hjort Seamount, R/V *Eltanin*, stn. 1964, 59°58'S, 155°31'W, in 2985–2992 m, 10 February 1967; paratype 3, USNM 886105 (figures 11–12, sex undetermined) Victoria Land, south of Scott Island Bank, R/V *Eltanin*, stn. 1939, 69°03'S, 179°41'E, in 3519–3596 m, 1 February 1967.

Other material examined: USNM 901317 (Figs 13–14, 1 specimen, sex undetermined) Victoria Land,

Moubray Bay, R/V *Eltanin*, stn. 2002, 72°18'S, 177°35'E, in 2005–2010 m, 11 January 1968; USNM 870610 (figures 8–10, 2 dead shells) Antarctic Peninsula, R/V *Eltanin*, stn. 1003, 62°41'S, 54°43'W, in 210–220 m, 15 March 1964.

Etymology: *papyrodes*—made from papyrus, referring to the thinness of the shell.

Remarks: The type series of *Obscuranella papyrodes*, n. sp., consists of four specimens, including one paratype that lacks a shell. All were collected living on the abyssal

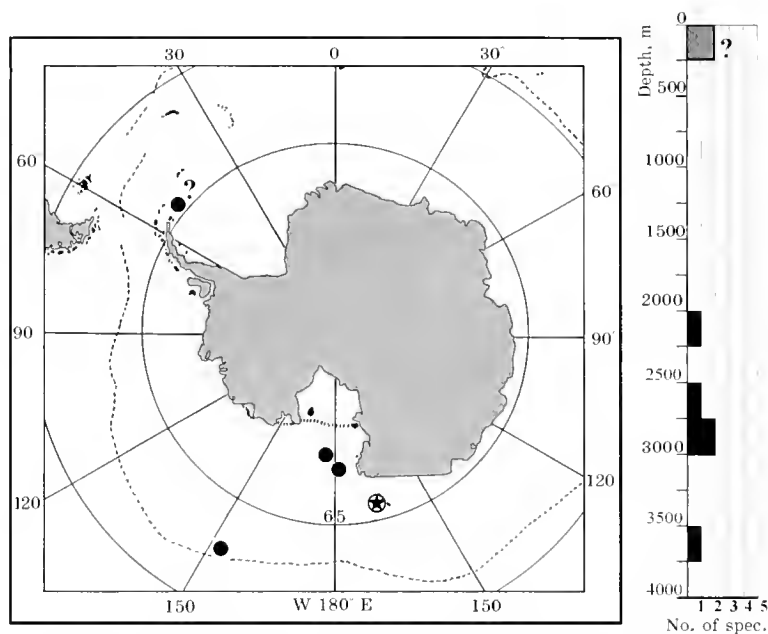


Figure 36. Geographic and bathymetric distribution of *Obscuranella papyrodes* new species.

plain off the Ross Sea. We are provisionally attributing three additional specimens to this species. One live-collected specimen (figure 13; USNM 901317), also from the abyssal plain off the Ross Sea, was considered by Dell (1990:199) to be congeneric but not conspecific with *Obscuranella papyrodes* n. sp. (which he identified as *Bathydromus obtectus* Thiele, 1912) because of its more elongated shell, longer siphonal canal, and angular shoulder. Even the earliest teleoconch whorls of this specimen appear angular because of a prevalent spiral cord along the periphery. This is exaggerated by a break in the shell and subsequent repair, evidenced by a thickened scar on the posterior part of the last whorl. The elongated shell and prominent siphonal canal are features shared with an immature paratype (paratype 3, figures 11–12) of *O. papyrodes*. This is the only specimen of *Obscuranella* with some portion of the early whorls intact (figure 14). The protoconch (2.0 mm estimated diameter) is eroded and replaced by a plug, but the earliest teleoconch whorls are well preserved and clearly show spiral cords.

Two dead collected shells (figures 8–10; USNM S70610), labeled as coming from upper slope depths (210–220 m) off the Antarctic Peninsula, closely match the morphology of this new species. We regard these specimens to represent *O. papyrodes*, but are skeptical of the accuracy of the locality data. Not only is this location on the opposite side of the Antarctic continent from all records of live collected *O. papyrodes*, it is also from much shallower depths (220 m vs. 2000+ m).

DISCUSSION

Obscuranella can readily be attributed to the superfamily Tonnoidea on the basis of its pyriform shell with large

aperture and conspicuous, if short siphonal canal; its extensible proboscis; its taenioglossan radula; its large salivary glands composed of morphologically differentiated anterior and posterior lobes and salivary ducts that pass through the nerve ring, as well as its undifferentiated oesophageal gland. It can be excluded from Ficidae, which was removed from Tonnoidea and elevated to superfamily status by Riedel (1994), by its high spire, lack of long siphonal canal, and also because Ficidae is characterized by small, tubular salivary glands. Similarly, it can be excluded from Laubierinidae, a family diagnosed by its monopectinate osphradium and excluded from Tonnoidea by Bandel and Riedel (1994), by its nearly symmetrical, bipectinate osphradium.

The shell of *Obscuranella* suggests an affinity with the deep-sea family Pisanianuridae (originally proposed as a subfamily of Ranellidae by Warén and Bouchet, 1990, transferred to Laubierinidae by Bandel and Riedel, 1994, and elevated to family status by Beu, 1998) by virtue of its smooth shell lacking regular varices and weakly defined anterior canal. The operculum of *Pisanianura* is slightly coiled but has a terminal nucleus, as does *Obscuranella*. However, the rachidian teeth of *Obscuranella* lack the lateral basal denticles present in Pisanianuridae (e.g. Warén and Bouchet, 1990:figs. 25–27), Bursidae (e.g. Warén and Bouchet, 1990:figs. 6, 8), Tonnoidea (e.g. Warén and Bouchet, 1990:figs. 9–14), and Laubierinidae (e.g. Warén and Bouchet, 1990:figs. 41–44), but absent in Cassidae (e.g. Warén and Bouchet, 1990:figs. 15, 16, 18), Personidae (e.g. Beu, 1998:fig. 15.140 E), and Ranellidae (e.g. Warén and Bouchet, 1990:figs. 28, 30, 32, 40).

The shell of *Obscuranella* somewhat resembles that of *Oocorys sulcata* Fischer, 1883 (Oocorythinae, Cassidae)

(see, eg. Bouchet and Warén, 1993:figs. 1936–1943), and some ranellids, such as *Argobuccinum pustulosum* (Lightfoot, 1786) (see e.g. Ben, 1998:fig. 15.12 D). The operculum of *Obscuranella* has a sharply pointed, terminal nucleus, and differs from the spirally coiled operculum of *Oocorys* (Warén and Bouchet, 1990: fig. 66). In adult *Argobuccinum* the nucleus of the operculum is subcentral, but in very young specimens of *A. pustulosum* (Warén and Bouchet, 1990:fig. 69) the nucleus is terminal. However, the operculum of *Obscuranella* is distinctive in its very small size, relative to the aperture, and in having straight, anteriorly converging margins.

The anatomy of *Obscuranella* is typically tonnoidean, most closely resembling that of the ranellid *Cymatium* (Houbrick and Fretter, 1969). *Obscuranella* can be distinguished anatomically from the Tonnoidea by its lack of a buccal gland, and from Pisanianuridae and Laubierinidae by its lack of long proboscis retractor muscles that pass through the nerve ring.

We assign this genus to the family Ranellidae because of its general similarity to *Argobuccinum* in shell form, radular morphology, and gross anatomy. Moreover, Ranellidae is the only tonnoidean family to occur in Antarctic waters—*Fusitriton magellanicus* (Röding, 1798), a species with a wide geographic range, has been taken from several stations in the Weddell and Ross Quadrants (e.g. USNM 896058, USNM 896103, USNM 896277, USNM 898520—see Polar Invertebrate Catalog <http://www.nmnh.si.edu/cgi-bin/wdb/iz/pci/form>). *Obscuranella papyrodes* represents the first record of Ranellidae from abyssal depths.

ACKNOWLEDGMENTS

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Host-tree selection by Florida tree snails, *Liguus fasciatus* (Müller, 1774), in Big Cypress National Preserve, Florida, USA

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ABSTRACT

It has frequently been suggested that the Florida tree snail, *Liguus fasciatus*, exhibit preferences for specific host trees, although most accounts of host-tree selection are based on anecdotal observations. We assessed the relative use of host trees in eight hammocks in the Big Cypress National Preserve for which the relative availability of each potential host-tree species was known. Based on a total of 1,464 tree snail observations on 21 species of host tree within our study plots, host trees were not used in proportion to their availability when the expected values are derived either from the number of trees or from basal area. Of the most common tree species on our study area, wild tamarind (*Lysiloma latisiliquum*) was consistently used in excess of its availability. Wild lime (*Zanthoxylum fagara*), was not a common tree species, but was also used far in excess of its availability. Pigeon plum (*Coccoloba diversifolia*) and gumbo-limbo (*Bursera simaruba*) were consistently used less than expected from their respective availabilities. Based on Akaike's Information Criterion (AIC), the most parsimonious loglinear model, after accounting for availability, was one that included only tree species effects. In contrast to the model selected using AIC, likelihood ratio tests indicated that there may also be differences among hammocks, but not in relation to a linear gradient of hurricane damage. We observed differences in length among 3-year-old snails on different host trees, and these differences were consistent with the hypothesis that host-tree selection reflects food availability. Snails found on host-tree species that were used in greater than expected frequency had the greatest length, those found on trees used less than expected frequency were the smallest, and those found in proportion to their availability were intermediate in length.

Additional key words: Big Cypress National Preserve, host tree, hurricane, *Liguus fasciatus*, tree snail, Florida, hammock.

INTRODUCTION

Snails of the genus *Liguus* are native to Cuba, Hispaniola, and Florida (Pilsbry, 1912). The Florida tree snail

Liguus fasciatus (Müller, 1774) is found within a restricted part of this range, primarily some islands within the Florida Keys, the Atlantic coastal ridge, Everglades National Park, and Big Cypress National Preserve. Primarily because of agricultural and urban expansion, only a few isolated populations remain outside of protected public lands and a few isolated islands in the Keys. Consequently, they are listed as a species of special concern by the state of Florida. Thus, understanding the relationship between snails and their habitat is essential for the conservation and management of remaining populations.

In the Everglades, *L. fasciatus* is found on islands of subtropical hardwood trees and scrub known as hammocks. Hammocks are widely scattered throughout South Florida and may be separated by water, sawgrass, or other habitat types such as pines. It is widely believed that Florida tree snails exhibit strong preferences for host trees, particularly smooth-barked trees upon which their algal food source can easily be grazed (Pilsbry, 1912). In particular, snails are suggested to exhibit preference for Jamaica dogwood (*Piscidia piscipula*) in the Florida Keys and wild tamarind (*Lysiloma latisiliquum*) on the mainland (Pilsbry, 1912), although most accounts of host-tree selection are based on anecdotal observations, and few quantitative data are available. Voss (1976) reported numbers of snails found on each tree species in 2 hammocks on the coastal ridge. However, he did not account for the availability of these host trees: thus, differential selection can not be reliably assessed. Brown (1978) is the only study of which we are aware that compared the use and availability of host trees, although this was restricted to 1 hammock in Everglades National Park. Here we assess the relative use of host trees in eight hammocks in the Big Cypress National Preserve for which the relative availability of each tree species was known.

Brown (1978) also hypothesized that differences in quantity and quality of food resources of different host-

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tree species may result in size differences among snails using different host trees, although she was unable to statistically confirm such differences. We tested this hypothesis by comparing size differences among snails found on host-tree species that were used (1) in greater than expected frequencies (selected), (2) did not differ from expected frequencies (neutral), and (3) in less than expected frequencies (avoided).

MATERIALS AND METHODS

Our study population was in Big Cypress National Preserve (BCNP). The Pinecrest area of the BCNP contains one of the largest remaining populations of Florida tree snails. Within BCNP, 136 hammocks have been individually identified and mapped (Pilsbry, 1946); a few others may exist that have not been identified. We selected 8 of the 136 hammocks from this pool for our study sites. Eight hammocks provided a reasonable representation of the potential variability and represented a logistically feasible number of sites. This study was initiated to investigate the survival and movements of Florida tree snails following Hurricane Andrew. Hurricane Andrew crossed southern Florida from east to west on 24 August 1992. The eye of the storm passed along the southern boundary of our study area creating a decreasing latitudinal gradient of damage toward the north with increasing distance from the eye. Because we were interested in the potential effects of Hurricane Andrew, we also wanted our study sites to reflect the latitudinal gradient of hurricane impacts. Consequently, we divided the initial pool of hammocks into 4 zones reflecting clusters of hammocks positioned along a gradient from little or no hurricane impact to severe impact (Bennetts *et al.*, in press). There also exists considerable variability in the size of these hammocks, which we believed could have greatly influenced their susceptibility to damage by Hurricane Andrew and consequently affected tree snails. Therefore, we digitized each hammock from USGS 7.5-minute ortho photos and used a Geographic Information System (GIS) to estimate the approximate size of each hammock. We then used stratified random sampling to select 1 hammock of greater size than the median size and 1 hammock of lesser size from each of the 4 impact zones. Thus, our sample reflected the latitudinal gradient of hurricane damage and was balanced among larger and smaller hammocks.

We established two 80 m² study plots (sub-samples) in each hammock. These plots were randomly located in parts of the hammock where tree snails occurred. The center of each plot was marked with a steel rod and we subsequently marked all trees with a diameter at breast height (DBH) > 5 cm within a 5 m radius of the plot center. We recorded the species and DBH of each live tree within these plots.

During each of seven sampling occasions, we searched for all tree snails within each plot, and as part of a concurrent study on movements (Bennetts *et al.*, in press), for marked snails within an extended radius of approxi-

mately 20 m around the plot. Sampling was conducted each autumn and spring from autumn 1993 through spring 1996. Our sampling occasions were intended to reflect the biology of the animal and to minimize the potential for handling to influence a snail's survival. Our spring sampling occasion was conducted as soon as possible after emergence of the snails from aestivation. This coincided with the onset of the annual rainy season. At this time snails begin to put on new growth, which becomes very fragile as it extends as a thin layer from the previous growth. Thus, our sampling was intended to precede the period during which time shells are fragile, although some growth had occurred on some snails. Our autumn sampling occasion coincided with the onset of the dry season just prior to aestivation. At this time the summer's growth had been terminated, the shells had thickened, but the animals had not yet entered aestivation. Animals that were visually determined to be in aestivation (<1%) by presence of an epiphragm (dried mucus membrane across the aperture) were not disturbed. For each snail we determined its age from annual growth scars (Tuskes, 1981), measured its length from tip to tip parallel to the axis and width perpendicular to the axis at its widest point. We also recorded the host tree from which it was collected. We then returned each snail to the same host tree by placing them in a conical paper cup attached to the trunk of the tree.

Statistical Analyses: As a preliminary analysis we tested for an association between use and availability of all host-tree species within our study plots using a chi-square goodness of fit test. This was done for a descriptive account of the relative selection of all host species; however, cells having expected values <5 could produce unreliable test statistics (Cochran, 1954). Thus, for further analyses including additional effects of hammock of hurricane influence, we pooled cells with expected values <5 into an "other" category.

We tested whether host trees were used in proportion to their availability using a loglinear model. To account for host tree availability we used either the log number of trees, or the log basal area as an offset (Agresti, 1990; McCullagh and Nelder, 1989). Thus, the frequency of snails observed was modeled per available number and basal area of each species. We used basal area in addition to the number of trees because the surface area of trees are generally related to its basal area (Whittaker and Woodwell, 1967; Brown, 1978). We then tested whether the number of snails was influenced by tree species, and then whether this association differed among hammock or hurricane zone.

Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973; Shibata, 1989), which is defined as: $-2\ln(\mathcal{L}) + 2np$, where $-2\ln(\mathcal{L})$, represents the likelihood ratio between the given model and a corresponding saturated model; thus, represents a measure of model fit. The second term, $2np$, is the number of parameters estimated in the model and can be viewed as a cost for adding excessive parameters that do

Table 1. Common and scientific name of the host-tree species within our study plots. Also shown are the total number of trees, total basal area, and total number of snails observed for each species.

| Common name | Scientific name | Acronym | No. trees | Basal area | No. snails |
|-----------------|--------------------------------------|---------|-----------|------------|------------|
| Cocoplum | <i>Chrysobalanus icaco</i> | Ci | 1 | 174 | 1 |
| Dahoon holly | <i>Ilex cassine</i> | Ic | 2 | 365 | 21 |
| Gumbo limbo | <i>Bursera simaruba</i> | Gl | 26 | 5423 | 85 |
| Hackberry | <i>Celtis laevigata</i> | Cl | 2 | 212 | 15 |
| Inkwood | <i>Exothea paniculata</i> | Ep | 2 | 93 | 3 |
| Lancewood | <i>Nectandra coriaceae</i> | Nc | 25 | 2362 | 52 |
| Wild lime | <i>Zanthoxylum fagara</i> | Zf | 1 | 79 | 20 |
| Live oak | <i>Quercus virginiana</i> | Qv | 2 | 480 | 2 |
| Wild tamarind | <i>Lysiloma latisiqua</i> | Ll | 128 | 41820 | 983 |
| Mastic | <i>Mastichodendron foetidissimum</i> | Mf | 2 | 711 | 8 |
| Paradise tree | <i>Simarouba glauca</i> | Sg | 2 | 240 | 11 |
| Pigeon plum | <i>Coccoloba diversifolia</i> | Cd | 80 | 9489 | 145 |
| Poisonwood | <i>Metopium taxifera</i> | Mt | 2 | 252 | 5 |
| Pond apple | <i>Annona glabra</i> | Ag | 1 | 47 | 1 |
| Red bay | <i>Persea borbonia</i> | Pb | 1 | 620 | 9 |
| Red stopper | <i>Eugenia rhombea</i> | Er | 1 | 22 | 1 |
| Satinleaf | <i>Chrysophyllum oliviforme</i> | Co | 1 | 85 | 1 |
| Simpson stopper | <i>Myrcianthes fragrans</i> | Mf | 6 | 723 | 18 |
| Strangler fig | <i>Ficus aurea</i> | Fa | 1 | 90 | 2 |
| White stopper | <i>Eugenia axillaris</i> | Ea | 7 | 273 | 9 |
| Willow bustic | <i>Bumelia salicifolia</i> | Wb | 19 | 2646 | 72 |

not contribute substantially to the overall model fit. Thus, AIC indicates an appropriate balance between precision and bias (i.e., over and under-fitting the model) from a set of candidate models (Burnham and Anderson, 1998). In contrast to AIC, which is used as an optimization tool for comparison among models, we also used likelihood-ratio tests (LRTs) to test for specific effects of interest (Lebreton *et al.*, 1992; Burnham and Anderson, 1998).

The selection of host trees may be influenced by the quantity and quality of food resources (Brown, 1978), which may in turn result in size differences of snails using different host trees. We tested this hypothesis by comparing size differences among snails found on host-tree species that were used (1) in greater than expected frequencies (selected), (2) did not differ from expected frequencies (neutral), and (3) in less than expected frequencies (avoided). We compared the size of snails (i.e., length and width) within each age class among host-tree species using a fixed-effects analysis of variance (ANOVA) model. For this analysis we were not concerned with the availability of host trees, only species. Consequently, we included all snails encountered on our study hammocks for this analysis, regardless of whether they were found within the designated plots (used to compare selection with availability) or the extended radius (used for analyses of movement) (Bennetts *et al.*, in press). However, we restricted our sample to snails collected during the autumn sampling occasion to minimize any confounding attributable to variation in the extent of new growth during spring.

RESULTS

We observed 1464 tree snails on 21 host-tree species within our study plots (Table 1). Host trees were not used in proportion to their availability when the expected values are derived either from the number of trees ($\chi^2 = 554.18$, 20 df, $P < 0.001$) or from basal area ($\chi^2 = 296.14$, 20 df, $P < 0.001$). Of the common tree species on our study area, wild tamarind was consistently used in excess of its availability (figure 1). Wild lime (*Zanthoxylum fagara*), was not common, but our observations indicated that it was used far in excess of its availability, regardless of which measure of availability was used. Although the sample for this species used in our analysis included only 1 tree, we observed others on our study area that had similar high use. In contrast, pigeon plum (*Coccoloba diversifolia*) and gumbo-limbo (*Bursera simaruba*) were relatively common, but were consistently used less than expected. Willow bustic (*Bumelia salicifolia*) and lancewood (*Nectandra coriaceae*) also were relatively common in our study plots, but our results were conflicting for these species. In relation to the number of trees, willow bustic was used slightly less than expected whereas, based on basal area, it was used slightly more than expected. Lancewood was used less than expected in reference to the number of trees, but in proportion with its availability in relation to basal area.

After pooling cells with low expected values, the most parsimonious model based on AIC included only tree species effects ($\chi^2 = 101.05$, 5 df, $P < 0.001$). Departures from expected values were consistent with our preliminary analysis in that wild tamarind was used in greater proportion than expected from its availability; pigeon

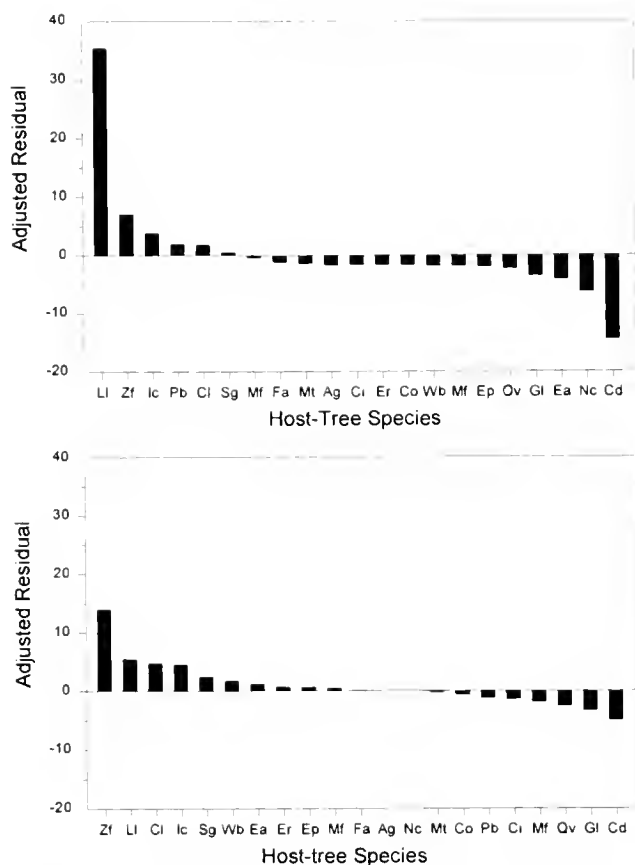


Figure 1. Adjusted residuals (Haberman 1973) from goodness-of-fit test between the number of snails found on different host-tree species in relation to their availability. Host-tree species are displayed in rank order from selected in greatest proportion relative to its availability to least. Expected values were derived based on the number of trees of a given species (top) and the total basal area for a given species (bottom). Positive residuals >1.96 indicate use greater than expected from availability and residuals <-1.96 indicate use less than expected from availability.

plum and gumbo limbo were used less than expected. Lancewood and willow bustic were intermediate as was our "other" class. In contrast to the model selected using AIC, LRTs indicated that there may have been a species \times hammock interaction ($\chi^2 = 110.36$, 31 df, $P < 0.001$), but not a species \times hurricane zone interaction ($\chi^2 = 9.32$, 5 df, $P = 0.097$). Thus, our data indicated that selection of host-tree species may have differed among hammocks, but this difference was not in relation to a gradient of hurricane damage.

We found size (length) differences among snails found on host tree species only for 3-year-old snails ($F_{2, 348} = 3.42$, $P = 0.034$) (figure 2). Of these, the length of snails was highest for snails found on host trees that were used in greater frequency than their availability (selected) and lowest for snails found on host trees that were used less than their availability (avoided). Snails found on host trees that were not out of proportion to their availability

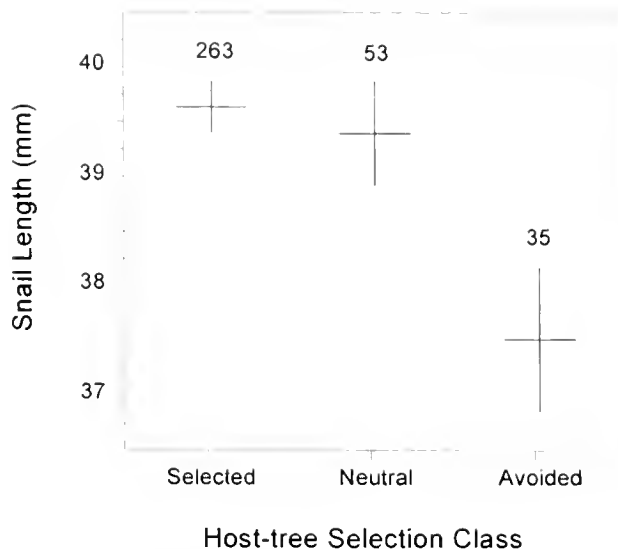


Figure 2. Mean length (\pm SE) of 3-year-old tree snails found on host-tree species that were used in excess of their availability (Selected), less than their availability (Avoided) and did not differ from availability (Neutral). Sample sizes are shown for each group.

(neutral) were intermediate in length, but did not differ from either of the other groups (Fisher's Least Significant Difference, $P > 0.05$). We did not find differences in width among any host-tree species for any age class at the $\alpha = 0.05$ level.

DISCUSSION

Our data are consistent with previous reports of wild tamarind being used in excess of availability; although the degree of this association is highly sensitive to what measure is used to derive the expected values for availability. When the expected value is derived from basal area, the association is much weaker than when the expected value is derived from the number of trees. Expected values derived from basal area probably better reflect the surface area available for foraging. The number of stems would be important if the probability of a dispersing snail moving to a given tree is dependent on it encountering a trunk on the ground, although most inter-tree movement on our study area probably was via intertwined foliage. Brown (1978) reported a remarkably similar result in Everglades National Park. She reported an overall significant test statistic based on both number of tree stems and estimates of bark surface area, although the relationship was substantially weaker based on bark surface area. Regardless of the statistical significance, 983 of 1464 (67%) of all snails we observed were found on wild tamarind. Voss (1976) reported a similar estimate of 34 of 50 (65%) for 1 hammock in the eastern Everglades near Miami, and Brown (1978) reported 209 of 395 (52%) in another location in Everglades National Park. Although other trees may be preferentially selected if available, wild tamarind was the most abundant and

most used host tree within the Big Cypress National Preserve, which is probably also the case in most of the mainland habitats. Thus, wild tamarind is clearly an important component of tree-snail habitat in this region.

Although our model selection did not support that host-tree selection differed among hammocks, an LRT did indicate a species by hammock interaction effect. Hammocks differed with respect to which host tree species were present, which likely reflects inter-hammock differences in attributes such as size, soils, and hydrologic regimes. Thus, the interaction effect we observed could have been attributed to these differences in species composition, but our data are insufficient to evaluate such effects with much reliability.

Bias due to visibility of snails was not accounted for by our approach. This effect would have been most influenced by dense foliage obscuring snails from view. For most host-tree species, we believe that this bias was negligible, especially because of reduced foliage as a result of Hurricane Andrew. However, one notable exception was pigeon plum, which often had very dense foliage making it difficult to detect snails. Thus, we suspect that our data indicating that this host tree species was underutilized may have been, at least in part, an artifact of detection bias.

Although our data are far from conclusive, they are consistent with Brown's hypothesis that there may be an association between selection of different host trees and size of the snails. We found size differences only among 3-year-old snails. However, even our relatively large sample sizes tend to become quite small once partitioned by age and host tree species. Florida tree snails exhibit most growth during their first 2–3 years, after which growth slows dramatically (Tuskes, 1981). Thus, 3-year-old snails probably represent a peak of cumulative growth, and are a likely age class to observe size differences. For this age class, snails found on host-tree species used less than expected were smallest in length, those found on trees used in excess of availability were the largest in length, and those found in proportion to their availability were intermediate in length.

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The development of three heterobranch mollusks from California, USA

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ABSTRACT

The development of *Odostomia altina*, *Turbonilla* sp., and *Williamia peltoides* from California, is typical of heterobranch mollusks. They all produce small eggs (about 60 μm) that are individually encapsulated and embedded in gelatinous egg masses. The capsules are connected by chalazae. Cleavage is unequal and gastrulation occurs by invagination. Planktotrophic larvae hatch at shell lengths of 120–150 μm .

Additional key words: Pyramidellidae, *Turbonilla*, *Odostomia*, gastropod development, *Williamia*.

INTRODUCTION

Although lower heterobranchs and marine pulmonates are common in shallow marine waters, their development remains largely undescribed. Knowledge of their development may be useful and important because developmental features such as the structure of egg masses, cleavage type, presence of the larval pigmented mantle organ (PMO), and hydrophobic larval shells may be important characters for phylogenetic studies (Robertson, 1985; van den Biggelaar, 1996; van den Biggelaar and Haszprunar, 1996; Collin, 1997). Additionally, there are a variety of interesting trends in the evolution of cleavage patterns (Freeman and Lundelius, 1992; van den Biggelaar and Haszprunar, 1996) and heterochronies in larval morphologies (Page, 1994) whose documentation could benefit from more extensive phylogenetic sampling.

Herein I describe the development of two pyramidellid and one siphonariid pulmonate species from the Californian coast. All animals were collected by hand in the summer of 1997 and kept in small dishes in the laboratory where they laid egg masses. Egg masses were observed daily until hatching, but no attempt was made to raise the larvae to metamorphosis.

RESULTS

Odostomia altina Dall and Bartsch, 1909
(Table 1)

Large numbers of *Odostomia altina* were found on the shells of *Haliotis corrugata* collected at a depth of 10 m from Point Loma, California (29°40'N, 117°20'W). Specimens are deposited at the Field Museum of Natural History (FMNH 282369 and 282370) and were identified by comparison with the original species description and illustrations in (Dall and Bartsch, 1909). There were as many as 50 adult pyramidellids and numerous egg masses on one abalone. Egg masses were typical of other pyramidellids: Single eggs are enclosed in albumin-filled oval capsules that are embedded in a clear sticky gelatinous mass. The capsules are connected by thin extensions of the capsular covering called chalazae (see Robertson, 1985; Collin and Wise, 1997 for detailed description). A timetable of development is given in Table 1.

The round, white eggs are 60 μm in diameter (mean = 60.83 μm ; sd = 1.39 μm ; n = 31; eggs from 3 egg masses) the inner capsule diameter is 150 μm (sd = 8.11 μm ; n = 19) and the outer capsule diameter is 176 μm (sd = 6.992 μm ; n = 10). First cleavage is unequal and at the 4-cell stage the two largest cells are adjacent, as are the two small ones. Several embryos were observed in a 3-cell stage, which suggests that second cleavage is not synchronous. There is no polar lobe and third cleavage is unequal. The round blastula gradually flattens and invaginates to form a horseshoe shaped gastrula. During subsequent development the embryo grows to fill the capsule and the larval organs differentiate. Planktotrophic larvae hatch after about 7 days (Table 1) with 130 μm (mean = 130.33 μm ; sd = 8.55 μm ; n = 15; egg masses from two females) smooth, left-handed, hydrophobic shells. Each larva has a well-developed metapodial ten-

Table 1. Development schedule for *Odostomia altina* at 22–24°C.

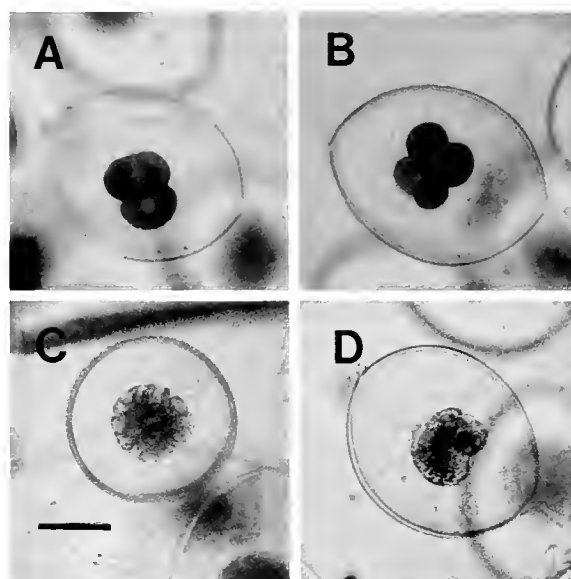
| Age | Stage |
|----------|--|
| >3 hours | 2-cells |
| 5 hours | 4-cells |
| 12 hours | 64-cells |
| 1 day | blastula |
| 1.5 days | gastrulation by invagination |
| 3 days | just moving, foot and velum anlagen visible |
| 5 days | red-yellow PMO visible, shell operculum and statocysts |
| ~7 days | hatching at 130 μ m |

tacle and statocysts, but no detectable heartbeat, and no eyes. The larval PMO consists of two parts: A round red central part and an additional semi-transparent yellow lobe on one side. Observation of the yellow lobe under the dissecting microscope is difficult, but the structure can be seen easily under a compound microscope.

Turbonilla sp.

(Figures 1, 2, table 2)

One adult of an unknown species of *Turbonilla* was collected on the high mid-intertidal zone at Alegria, California (34°28'N, 120°17'W) in July 1997. The species identification is uncertain because *Turbonilla* taxonomy is especially difficult and the single specimen could not be unambiguously assigned to any Californian species. The current taxonomy of Californian pyramidellids assigns all species with axial-ribbed shells to the genus *Turbonilla* (Dall and Bartsch, 1909). This snail laid one egg

**Figure 1.** Adult *Turbonilla* sp. Shell length is 6 mm.**Figure 2.** Early developmental stages of *Turbonilla* sp. A. 2-cell stage at the beginning of second cleavage, the cells are clearly not equal in size. B. 4-Cell stage. C. blastula. D. gastrula, showing the invagination typical of heterobranch development. Scale bar = 50 μ m.

mass of about 100 eggs in the laboratory and development was followed until hatching (table 2 and figure 2). The egg mass consisted of capsules containing one white egg surrounded by clear albumin, connected together by chalazae and embedded in a clear sticky gel. The egg diameter was 65.5 μ m ($n = 10$, $sd = 1.97$ μ m) and the capsule length was 187.8 μ m ($n = 10$, $sd = 6.67$ μ m). The chalazae are thicker and less twisted than in *O. columbiana* Dall and Bartsch 1907 (Collin and Wise, 1997). First cleavage is slightly unequal but by the 4-cell stage the blastomere inequality is very subtle. The early cleavages do not produce a polar lobe. The polar bodies are clearly visible throughout development because the albumin is transparent. After 24 hours the embryos form flattened blastulas, which begin to invaginate at about 40 hours. Gastrulation continues by invagination for the next day. By the fourth day the foot and velum anlagen are visible. On the fifth day the embryos begin to move

Table 2. Developmental schedule for *Turbonilla* sp. at 16–18°C.

| Age | Stage |
|----------|---|
| 7 hours | 2-cells |
| 24 hours | blastula |
| 2–3 days | gastrulation by invagination |
| 4 days | just moving, foot and velum anlagen visible |
| 5 days | shell and velum differentiated. Embryo fills 1/4 of the capsule |
| 6 days | black PMO visible |
| 9 days | embryo fills the capsule |
| 11 days | hatching at 152 μ m |

and they fill about a quarter of each capsule. By the next day the black PMO is visible on the right side just posterior to the velum. The embryo grows to completely fill the capsule, before hatching. Shell length at hatching is 152 μm ($n = 14$; $\text{sd} = 2.37 \mu\text{m}$; from a single egg mass). The shell is hydrophobic, left-handed and the larva has no heart or eyes but has a well-developed metapodial tentacle on the foot. The planktotrophic larvae swim actively.

Williamia peltoides (Carpenter, 1864)

Several adult *W. peltoides* (Carpenter, 1864) were collected in the subtidal zone ($\sim 10 \text{ m}$), on hard substrates, in the vicinity of Santa Barbara, California ($34^{\circ}28'N$, $120^{\circ}17'W$). Voucher specimens are deposited at the Bailey-Matthews Shell Museum, Sanibel, Florida (BMSM 4999). *Williamia* species are unusual among marine pulmonates because they are predominately subtidal. Adults produced several egg masses in dishes in the laboratory.

The structure of the egg masses is very similar to those of the pyramidellids. The eggs are each individually enclosed in a coating of albumin inside an oval capsule. The capsules are connected with chalazae and are embedded in a gelatinous mass. The capsules are 147 μm in length (mean = 147.7 μm ; $\text{sd} = 3.4 \mu\text{m}$; $n = 11$). Unfortunately uncleaved eggs and early cleavage stages were not observed. Gastrulation occurs via invagination forming a horseshoe-shaped gastrula that is 69 μm in diameter ($d = 69.28 \mu\text{m}$; $\text{sd} = 3.4 \mu\text{m}$; $n = 7$; from one egg mass). Further development progressed as in the pyramidellids. However, no pigmented PMO develops: I could not determine if there was no PMO or if the structure was present but not pigmented. There is some reddish pigmentation along the suture of the larval shell, but the larval body was pigmentless. After 9 days at $18\text{--}22^{\circ}\text{C}$ the larvae hatch at a length of 126 μm (length = 126.0 μm ; $\text{sd} = 5.58 \mu\text{m}$; $n = 10$). The planktotrophic larvae have a hydrophobic smooth left-handed shell. There is still no pigmented PMO, no eyes, and no metapodial tentacle but the statocysts are clearly visible.

DISCUSSION

These observations are the first descriptions of intracapsular development for species in the genera *Williamia* and *Turbonilla*.

The features of pyramidellid development described here generally agree with previous descriptions of pyramidellid development. Because *Turbonilla* and *Odostomia* are distantly related genera within the Pyramidellidae (Wise, 1996), characters shared by the species described here and *O. columbiana* (Collin and Wise, 1997) may be typical of pyramidellid development in general. All three species have small eggs, unequal cleavage, gastrulation by invagination, and hatch with smooth, left-handed, hydrophobic shells, a metapodial tentacle, distinct PMO, but without eyes or a larval heart. The color

of the larval PMOs varies among species as does the color of the adult PMO (Robertson, 1985).

The development of *Williamia peltoides* is strikingly similar to pyramidellid development. The structure of the egg masses is indistinguishable from that of the pyramidellids. Hatching larvae are distinct in their lack of a metapodial tentacle and pigmented PMO and the small area of shell pigment. These results are in agreement with Robertson's (1985) conclusion that larval PMOs are not present in pulmonates while chalazae and heterostrophy are common. The reddish pigment along the shell suture is also found in larvae of *Siphonaria* sp. from New Zealand (pers. obs.).

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Diminishing species richness of mollusks in Oneida Lake, New York State, USA

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ABSTRACT

Between 1915 and 1917, F. C. Baker studied the molluscan fauna of Oneida Lake, a shallow, eutrophic lake in central New York State. He listed 41 living taxa, of which two gastropods, *Bithynia tentaculata* (Linnaeus, 1758) and *Pleurocera acuta* (Rafinesque, 1829), were then recent introductions. In 1967–68, John Forney and I (Harman and Forney, 1970) surveyed Oneida Lake, visiting Baker's original collecting sites. We tallied 35 living taxa dominated by the introduced European *B. tentaculata*. In 1992–95, I again made extensive collections of mollusks finding a total of 24 living taxa dominated by *Dreissena polymorpha* (Pallas, 1771), the then recently introduced Eurasian zebra mussel. Fifty percent of Baker's original eulittoral collection sites could not be found. An average 1 m² area in 1992–95 included 6708 individuals of *D. polymorpha*, 60 of *B. tentaculata* and 2 of the unionid bivalve *Elliptio complanata* (Lightfoot, 1786). Molluscan species richness was reduced by 15% between 1917 and 1968, a trend concurrent with the increase in abundance of *Bithynia*. Species richness was further reduced by 31% between 1968 and 1995, as human activities impacted eulittoral habitats and *D. polymorpha* colonized Oneida. The total decrease in species richness between 1917 and 1995 was of 42%. Since 1996 no living unionids have been observed in the lake.

Additional key words: Exotic introductions, habitat destruction, freshwater, gastropods, bivalves, *Bithynia tentaculata*, *Dreissena polymorpha*.

INTRODUCTION

Oneida Lake is a eutrophic lake in central New York State, with about 233 km² in surface area and a maximum depth of 16.8 m. It is located in a depression on the low, open relief of the Ontario Lake Plain in the Oswego River drainage basin (figure 1). The lake is oriented with its length parallel to that of the prevailing westerly winds. It mixes throughout the ice-free period, with thermal stratification occurring only ephemerally during wind-free periods (Harman and Forney, 1970). Tributaries to Oneida drain densely populated areas of Onondaga Limestone and fertile soils. As a result, the lake has been considered one of the most naturally productive in the world (Mozley, 1954). Historically, popu-

lations of algae and aquatic vascular plants have thrived in the shallow waters along the shoals, beaches, and islands, on diverse eulittoral substrates providing food and cover for a varied and abundant molluscan fauna (Harman and Forney, 1970).

Central New York has a diverse molluscan fauna derived from species immigrating from Atlantic coastal rivers, the Mississippi River drainage (Interior Basin), and the Great Lakes, soon after the retreat of the last Pleistocene glaciers (Clarke and Berg, 1959). Oneida Lake is unique due to its central position on the New York Barge Canal system and natural waterways (figure 1), which have continued to provide access to immigrating organisms from the early 1800s. Since then, mollusks from Lake Erie and the Ohio River basins in the west, and from the Atlantic coastal drainage in the southeast (via the Mohawk and Hudson drainage basins) have found their ways to Oneida Lake. Headwaters of several watercourses flowing from the Appalachian highlands in the southern Oswego system join the Susquehanna drainage via through-valleys, which facilitates dispersal of aquatic organisms. The Oswego River drains Oneida flowing to Lake Ontario and, via the St. Lawrence River, joins Lake Champlain and other northern waterways, thus providing access to and from North Atlantic drainage systems.

During 1915–17, F. C. Baker studied the macrobenthos in Oneida Lake, concentrating on the molluscan fauna excepting the fingernail clams (Sphaeriidae) (Baker, 1916a, b, c; 1918a, b, c, d). His research on Oneida's Lower South Bay is among the earliest quantitative studies of freshwater macrobenthos in North America (Baker, 1918c). Baker studied Oneida because of its great diversity of mollusks. In 1967 and 1968 I (Harman and Forney, 1970) conducted, as part of a survey of the gastropods of the Oswego River drainage basin, a qualitative study of the molluscan fauna of Oneida Lake. In the summer of 1967, Forney (Harman and Forney, 1970) repeated Baker's (1918c) quantitative work in Lower South Bay as part of a macrobenthic monitoring program carried out by Cornell University.

The introduction of zebra mussels (*Dreissena polymorpha*) into Oneida Lake in 1990 (Mitchell *et al.*, 1996)

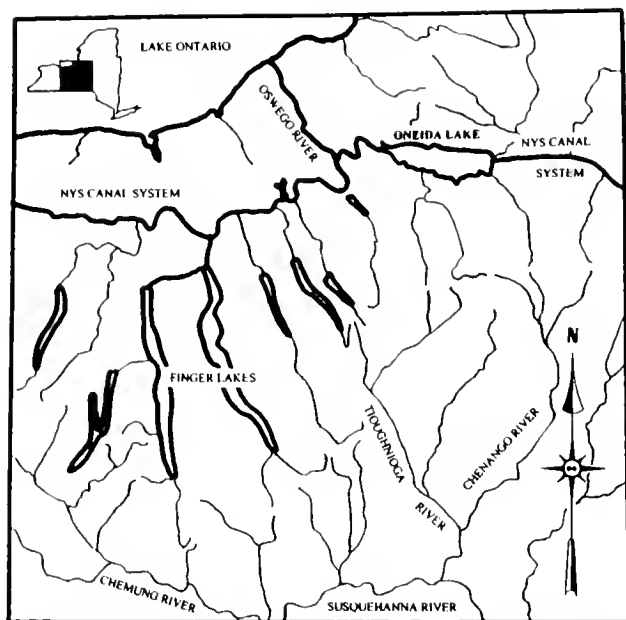


Figure 1. Central New York State showing Oneida Lake and routes of immigrating mollusks.

has had important impacts on water clarity by reducing phytoplankton standing crops. It also appears to be affecting the distribution and abundance of aquatic vascular macrophytes (E. L. Mills, pers. comm.). The irruption of the *Dreissena* population was expected to have tremendous impacts on the molluscan fauna (e.g., Nalepa *et al.*, 1991; Ricciardi *et al.*, 1995; Schloesser *et al.*, 1996). That concern prompted my return to Oneida during 1992–95 to determine the status of the molluscan community. I effectively repeated my (Harman and Forney, 1970) 1967–68 qualitative work and in 1993 did a quantitative study in Lower South Bay in an attempt to repeat Baker's 1915–18 studies (1915c) as well as Forney's 1967 work (Harman and Forney, 1970).

This paper describes the changes in the molluscan fauna since 1915, showing evidence of a constant reduction of species richness concurrent with destruction of eulittoral habitats and invasions of immigrating mollusks.

MATERIAL AND METHODS

In 1915–17, during the summer months, Baker obtained quantitative samples in Lower South Bay using a sieve, flattened on one edge, attached to a wooden pole, to collect bottom samples of about 10^2 cm^2 . A variety of larger dredges were used in deeper water. A square metal frame, viewed through a glass-bottomed bucket, was used to estimate densities of large snails and bivalves. Collections were made while wading, or from a boat (1915c). Water depths in Lower South Bay are such that these methods allowed him to sample all areas of the bay. Baker's samples at each collecting site approximated 10^2 cm^2 . He used varying numbers of replicates, typically

2–6. All his computations were presented using 10^2 cm^2 (16 in^2) as the basic unit.

My 1967–68 qualitative survey was made throughout the lake in an attempt to sample every habitat suitable for mollusks. Samples were retrieved from inorganic substrates strained through a sieve or handpicked with forceps in shallow water. Vegetation was collected and dried over containers for retrieval of desiccating organisms. Collections from deeper water were done similarly using SCUBA. Forney contributed several Ekman grab samples to that study. Forney's replication of Baker's quantitative study in Lower South Bay, again during the summer months, used Baker's methods as mentioned above. However, he relied more on standard Ekman grabs. Calculations were based on 10^2 cm^2 sample areas to facilitate comparison with Baker's work. Eleven of Baker's original sample sites (out of a total of 140) were lost due to artificial modifications of the shoreline.

In 1992–95 the same methodologies were used for the qualitative work, over the same time period that Forney (Harman and Forney, 1970) had covered in 1967–68. The 1992–95 quantitative work in Lower South Bay involved Ekman samples in deep water and square metal frames in eulittoral waters. Calculations were based on 1 m^2 sample size. Information is presented using this size, as well as 10^2 cm^2 for comparison with the earlier studies. It should be noted that when converting to 1 m^2 from the earlier 10^2 cm^2 sample size, diversity is potentially underestimated since widely separated large individuals such as unionids often encountered in the former are rarely found in the latter samples, and thus never appear in the data set. Only 71 of Baker's 140 original sites were still in existence in the recent survey. All taxonomic nomenclature herein has been updated according to Turgeon *et al.* (1998).

RESULTS AND DISCUSSION

Table 1 indicates the taxa that Baker encountered at the turn of the century. Baker's revised list includes 41 living molluscan taxa including the then recently introduced European snail *Bithynia tentaculata*, which had appeared around 1880 in Lake Ontario (Beauchamp, 1888). *Bithynia tentaculata* was assumed to have been introduced via ballast water in commercial seagoing vessels plying the Great Lakes (Baker, 1916b). The species was not abundant in Oneida Lake in 1915–17, but occurred in dense populations near the outlet at the west end. An average 10^2 cm^2 bottom sample made in 1917 contained 7 taxa, all consisting of native species (*Pyrgulopsis lustrica* (Pilsbry, 1890) (*Amnicola lustrica*, *A. lustrica* (var.) and *A. oncida* in Baker's original lists), *Stagnicola catascopium* (Say, 1867) (*Galba catascopium* of Baker), *Gyraulus parvus* (Say, 1817) (*Planorbis parvus* of Baker), *Physella gyrina* (Say, 1821) (*Physa gyrina* of Baker), *P. integra* (Haldeman, 1841) (*Physa integra* of Baker), *Promenetus exacuus* (Say, 1821) (*Planorbis exacuus* of Baker), and *Valvata tricarinata* (Say, 1817)) (figure 2). A second introduction, *Pleurocera acuta*,

Table 1. The molluscan fauna of Oneida Lake; reference conditions, 1915–17 (modified from Baker, 1918).

Taxa

Bivalvia: Palaeoheterodonta

Margaritifera margaritifera (Linnaeus, 1758)
Elliptio complanata (Lightfoot, 1786)
Alasmidonta undulata (Say, 1817)
Pyganodon grandis (Say, 1829)
Pyganodon cataracta (Say, 1817)
Strophitus undulatus (Say, 1812)
Villosa iris (I. Lea, 1829)
Lampsilis radiata radiata (Gmelin, 1791)
Actinonaias limentina (Lamarck, 1819)

Gastropoda: Basommatophora

Physella gyrina (Say, 1821)
Physella integra (Haldeman, 1841)
Physella heterostrophia (Say, 1817)
Lymnaea stagnalis (Linnaeus, 1758)
Fossaria obrussa (Say, 1825)^a
Stagnicola elodes (Say, 1821)
Stagnicola emarginata (Say, 1821)
Stagnicola catascopium (Say, 1867)
Pseudosuccinea columella (Say, 1817)
Acella haldmani (W. G. Binney, 1867)
Helisoma anceps (Menke, 1830)
Phanorbella trivolvis (Say, 1817)
Planorbella campanulata (Say, 1821)
Gyraulus parvus (Say, 1817)
Gyraulus deflectus (Say, 1824)
Promenetus exacuus (Say, 1821)
Laevapex fuscus (C. B. Adams, 1841)
Ferrissia parallelus (Haldeman, 1841)
Ferrissia rivularis (Say, 1817)

Gastropoda: Caenogastropoda

Campeloma decisum (Say, 1817)
Viviparus georgianus (I. Lea, 1834)
Pleurocera acuta (Rafinesque, 1820)^b
Ammicula limosus (Say, 1817)
Pyrgulopsis lustrica (Pilsbry, 1890)
Pomatiopsis cincinnatiensis (I. Lea, 1840)
Probythinella emarginata (Kuster, 1852)
Somatogyrus depressus (Tryon, 1862)
Bithynia tentaculata (Linnaeus, 1758)^c
Valvata tricarinata (Say, 1817)
Valvata sincera (Say, 1824)
Valvata lewisi (Currier, 1868)
Valvata bicarinata (I. Lea, 1841)

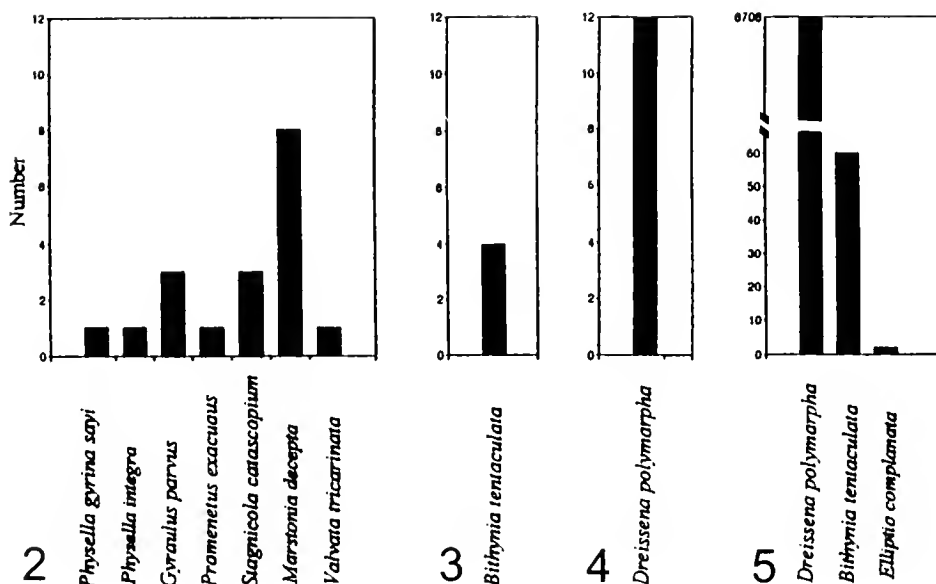
Total number of species: 41^a *Fossaria obrussa*, as used here includes *F. modicella*, (Say, 1825), *F. rustica* (I. Lea, 1841) and may include *F. parva* (I. Lea, 1841).^b *Pleurocera acuta* (Rafinesque, 1820) had invaded Oneida Lake via the Erie Canal system before Baker's 1915 work (Dazo, 1965).^c *Bithynia tentaculata* was apparently invading at the time of collection. Baker noted high densities in the outlet (Oneida River) very few in the Lake proper.**Figures 2–5.****Figure 2.** Dominant mollusks (individuals 10^{-2} cm²) in Lower South Bay, Oneida Lake, in 1915–17 (Baker, 1918c). In this, and figures 3 and 4, species occurring at a density of less than 0.5 individuals 10^{-2} cm² are not considered.**Figure 3.** Dominant mollusks (individuals 10^{-2} cm²) in Lower South Bay, Oneida Lake in 1967–68 (Harman and Forney, 1970).**Figure 4.** Dominant mollusks (individuals 10^{-2} cm²) in Lower South Bay, Oneida Lake in 1992–95.**Figure 5.** Dominant mollusks (individuals m⁻²) in Lower South Bay, Oneida Lake in 1992–95. Species occurring at a density of less than 0.5 individuals m⁻² are not considered.

Table 2. Molluscan species invading Oneida Lake followed by the approximate dates of introduction and origins.

| Taxa | Approximate dates of introduction | Origin |
|--|-----------------------------------|---|
| Bivalvia: Heterodonta | | |
| <i>Dreissena polymorpha</i> (Pallas, 1771) | 1986 | Eurasia, Great Lakes, Oswego River |
| Bivalvia: Palacoheterodonta | | |
| <i>Potamilus alatus</i> (Say, 1817) | 1920–1950 | Interior basin, Erie Canal system |
| <i>Leptodea fragilis</i> (Rafinesque, 1820) | 1920–1950 | Interior basin, Erie Canal system |
| <i>Ligumia recta</i> (Lamarck, 1819) | 1920–1950 | Interior basin, Erie Canal system |
| Gastropoda: Caenogastropoda | | |
| <i>Bithynia tentaculata</i> (Linnaeus, 1758) | 1910–1918 | Eurasia, Great Lakes, Oswego River |
| <i>Pleurocera acuta</i> (Rafinesque, 1820) | 1825–1915 | Interior basin, Erie Canal system |
| <i>Elimia livescens</i> (Menke, 1830) | 1920–1950 | Interior basin and/or Hudson river, Erie Canal system |
| <i>Elimia virginica</i> (Say, 1817) | 1920–1950 | Susquehanna Basin, through-valleys, Oswego Basin and/or Interior basin, Erie Canal system |
| Total number of species: 8 | | |

which had arrived via the Erie Canal from the west, was well established by the time Baker completed his studies (Dazo, 1965; Baker, 1918c).

When John Forney and I (Harman and Forney, 1970) collected in the 1960s, 35 taxa were found. Three gastropods, *Elimia livescens* (Menke, 1830), *E. virginica* (Say, 1817), and *Pleurocera acuta*, all in the family Pleuroceridae, were represented only by dead specimens. Three pearly freshwater mussels ((Unionidae), *Potamilus alatus* (Say, 1817), *Leptodea fragilis* (Rafinesque, 1820), *Ligumia recta* (Lamarck, 1819)) had immigrated from the Interior Basin (Clarke and Berg, 1959; Dazo, 1965). *Elimia virginica* was introduced into the Oswego watershed before the turn of the century (DeKay, 1843; Beauchamp, 1888). It is assumed that this species crossed the divide between the Susquehanna and Oswego River watersheds via through-valleys after small headwater lakes and wetlands on the divide were disturbed to provide water for the Erie Canal after its opening in 1825 (Harman, 1970). It also could have moved eastward along the Erie Canal from populations in the Interior Basin (Goodrich, 1942). *Bithynia tentaculata*, present in 1917, had become abundant by the 1960s. An average 10² cm² bottom sample in 1967 contained 4 individuals of *B. tentaculata* (table 2, figure 3).

Table 3 lists the taxa collected in 1915–17 (Baker, 1916a, b, c; 1918a, b, c, d) and in 1969 (Harman and Forney, 1970) that were not collected in the 1992–95 survey. Only 23 species of mollusks were present in 1992–95, two of them, *Ligumia recta*, and *Valvata sincera* Say, 1824 (Valvatidae), represented by dead specimens only. That represents a decrease of species richness of 42% since 1917. Collections made in 1996 and 1997 by faculty and students at the Cornell Biological Field Station on Oneida failed to find any living unionid bivalves (E. L. Mills, pers. comm.). Four of the species of mollusks found in 1993–95 were introductions. Of those, the population of *B. tentaculata* had declined greatly since the 1960s but was exceeded only by the exotic zebra mussel, *Dreissena polymorpha*. This Eur-

asian dreissenid was apparently carried through the Oswego River and New York State Barge Canal system by commercial and/or recreational navigation from the Great Lakes, where it was found in 1988 (Nalepa and Schloesser, 1993). Like *B. tentaculata*, *D. polymorpha* was supposedly transported in ballast water of ocean-crossing ships coming from Europe. An average 10² cm² bottom sample in 1993 contained 12 zebra mussels (figure 4). An average 1 m² sample collected at the same time and location included 6,708 specimens of *D. polymorpha*, 60 of *B. tentaculata*, and 2 of *Elliptio complanata* (Lightfoot, 1786) (*E. complanatus* of Baker) (figure 5). The tremendous increase results from large colonies of *D. polymorpha* initially associated with specimens of *E. complanata*, which were not encountered in the 10² cm² samples. These substrates are fine shifting sands practically devoid of zebra mussels, except where the comparatively widely disbursed unionids support their colonies.

Harman (1968a, b) proposed that the introduced *B. tentaculata* was able to displace the local representatives of the North American family Pleuroceridae in eutrophic environments. These observations were based on the distributions of *B. tentaculata*, *P. acuta*, *E. livescens* (*Goniobasis livescens* of Baker) and *E. virginica* in the Oswego River drainage basin in central New York (Harman and Berg, 1971). Like most caenogastropod snails of inland waters, the pleurocerids are periphyton grazers that rely on the benthic algal community as their main energy source. They typically inhabit waters supporting comparatively low populations of phytoplankton (Dazo, 1965). *Bithynia tentaculata* also is a grazer but in addition it can use planktonic algae which it filters from the water on specialized ctenidia (Jorgensen, 1966) potentially giving it an advantage in eutrophic waters such as Oneida Lake.

Observations in Oneida in the 1960s regarding the density of *Bithynia* on rocky shorelines, and on the observed behavior of pleurocerid snails associated with *B. tentaculata* in aquaria, substantiated these ideas. In

Table 3. Taxa lost (not collected alive since dates indicated) followed by assumed major contributing factors.

| Taxa | Last date collected | Contributing factors to decimation |
|---|---------------------|---|
| Bivalvia: Palaeoheterodonta | | |
| <i>Margaritifera margaritifera</i> (Linnaeus, 1758) | 1968 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Elliptio complanata</i> (Lightfoot, 1786) | 1995 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Alasmidonta undulata</i> (Say, 1817) | 1917 | Trophic alteration |
| <i>Pyganodon grandis</i> (Say, 1829) | 1995 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Pyganodon cataracta</i> (Say, 1817) | 1917 | Trophic alterations |
| <i>Strophitus undulatus</i> (Say, 1812) | 1917 | Trophic alterations |
| <i>Leptodea fragilis</i> (Rafinesque, 1820) | 1968 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Ligumia recta</i> (Lamarck, 1819) | 1968 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Villosa iris</i> (L. Lea, 1829) | 1917 | Trophic alterations |
| <i>Lampsilis radiata radiata</i> (Gmelin, 1791) | 1993 | Direct competition with <i>Dreissena polymorpha</i> |
| <i>Actinonaias ligmentina</i> (Lamarck, 1819) | 1917 | Trophic alterations |
| Gastropoda: Basommatophora | | |
| <i>Physella gyrina</i> (Say, 1821) | 1968 | Habitat destruction, trophic alterations |
| <i>Physella heterostrophia</i> (Say, 1817) | 1968 | Habitat destruction, trophic alterations |
| <i>Lymnaea stagnalis</i> Linnaeus, 1758 | 1917 | Habitat destruction, trophic alterations |
| <i>Stagnicola emarginata</i> (Say, 1821) | 1968 | Habitat destruction, trophic alterations |
| <i>Stagnicola catenescopium</i> (Say, 1867) | 1968 | Habitat destruction, trophic alterations |
| <i>Acella haldmani</i> (W. G. Binney, 1867) | 1968 | Habitat destruction, trophic alterations |
| <i>Gyrulus deflectus</i> (Say, 1824) | 1968 | Habitat destruction, trophic alterations |
| <i>Promenetus exacuus</i> (Say, 1821) | 1968 | Habitat destruction, trophic alterations |
| <i>Ferrissia rivularis</i> (Say, 1817) | 1917 | Habitat destruction, trophic alterations |
| Gastropoda: Caenogastropoda | | |
| <i>Cameloma decisum</i> (Say, 1817) | 1968 | Habitat destruction, trophic alterations |
| <i>Pleurocera acuta</i> (Rafinesque, 1820) | 1917 | Direct competition with <i>Bithynia tentaculata</i> |
| <i>Elimia vivenscens</i> (Menke, 1830) | ^a | Direct competition with <i>Bithynia tentaculata</i> |
| <i>Elimia virginica</i> (Say, 1817) | ^a | Direct competition with <i>Bithynia tentaculata</i> |
| <i>Pomatiopsis cincinnatiensis</i> (L. Lea, 1840) | 1968 | Habitat destruction, trophic alterations |
| <i>Probythinella emarginata</i> (Kuster, 1852) | 1917 | Habitat destruction, trophic alterations |
| <i>Somatogyrus deprussus</i> (Tryon, 1862) | 1917 | Habitat destruction, trophic alterations |
| <i>Valvata sinccra</i> (Say, 1824) | 1968 | Habitat destruction, trophic alterations |
| <i>Valvata lewisi</i> (Currier, 1868) | 1917 | Habitat destruction, trophic alterations |
| <i>Valvata bicarinata</i> (L. Lea, 1841) | 1917 | Habitat destruction, trophic alterations |
| Total number of species: 30 | | |

^a Empty shells collected in 1968, not collected in 1915; assumed introduction between 1920 and 1950.

aquaria enriched with planktonic algae, pleurocerids actively grazed over the substrate. Individuals of *B. tentaculata* remained in one spot, filtering algae from the water. Upon encountering specimens of *B. tentaculata*, pleurocerids were rebuffed by a violent twisting of the shell of that filter-feeder, which invariably caused the grazing snails to retract into their shells. They remained in that position for several minutes before resuming grazing. In situations with high densities of *B. tentaculata*, individual pleurocerids spent a large fraction of the time in defensive positions rather than feeding. In Oneida Lake in the 1960s, eulittoral cobble substrates were, in many areas, a solid mass of *B. tentaculata* (Harman and Forney, 1970). Under those conditions, all the species representing the family Pleuroceridae disappeared from the lake (Wisenden and Bailey, 1995). Nowadays, decreasing algal populations and increased water clarity have occurred concurrently with irrupting populations of *D. polymorpha*, while populations of *B. tentaculata* have diminished drastically.

A large number of the pulmonate gastropod species not found in the recent survey (e.g., one species of the planorbisid genus *Gyrulus*, three in the family Lymnaeidae, and two in the Physidae) are typical of eulittoral substrates and often associated with emergent vegetation. It is unlikely that these pulmonates are completely absent from Oneida, but their absence in the recent survey suggests drastic reductions in their populations corresponding with losses of that habitat due to shoreline development. Most of the shoreline has been modified as a result of the construction of breakwaters or rip-rap. Many of Baker's eulittoral sites appear to be buried under yards and beaches created by back-filling, which, by 1993–95, had destroyed considerable areas of emergent vegetation.

Other species of gastropods that were not found in the 1990s include several small prosobranchs in the family Hydrobiidae, which were typically abundant on submerged plants and nearby sub-littoral and deeper-water substrates. These and other gastropods that historically

have been present in abundance in Oneida Lake, were found in very low numbers in the recent survey. An exception, *Amnicola limosus* (Say, 1817) (*Amnicola limosa* of Baker), occurs in high densities in many littoral and sub-littoral areas. Changes in littoral vegetation and as yet unrecognized trophic alterations associated at least indirectly with colonization by *D. polymorpha* may be affecting these organisms (Stewart and Haynes, 1994; Howells *et al.*, 1996; Ricciardi *et al.*, 1997).

Seven of the 12 species of freshwater mussels found in Oneida since 1915 had been lost by 1993, and no living unionids have been observed since 1995 (table 3). These losses correspond to the introduction and establishment of *Dreissena polymorpha*. The literature documenting the loss of unionid species as a result of competition with *D. polymorpha* (Nalepa *et al.*, 1991; Griffiths, 1993; Ricciardi *et al.*, 1995; Schloesser *et al.*, 1996) and observations of the interaction between unionids and *D. polymorpha* in Oneida (E. L. Mills, pers. comm.) indicate that a large percent of this loss can be assumed to be attributed to interactions with *D. polymorpha*.

Since 1915–17, the endemic molluscan community in Oneida Lake has been greatly modified. Species richness has declined and the dominant faunal elements are now Eurasian in origin (figure 5). With the exception of recent changes since the introduction of zebra mussels, water quality in Oneida Lake has been consistent over the years (E. L. Mills, pers. comm.). It is assumed the observed changes are a result of biotic interactions with introduced taxa and loss of habitat due to human modifications of the eulittoral environment.

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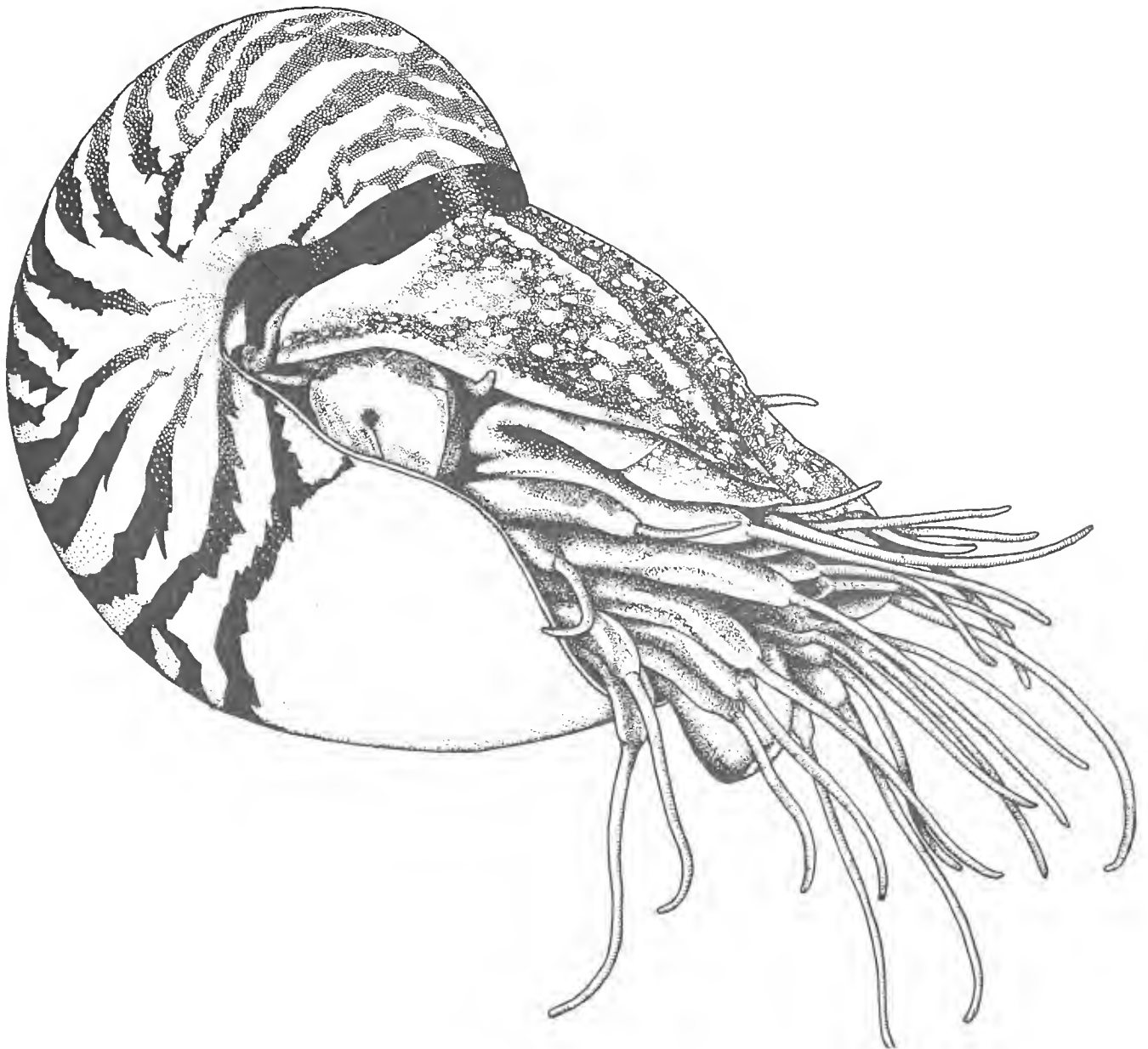
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Crepidula argentina (Gastropoda: Calyptraeidae), a new species from the littoral of Argentina

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ABSTRACT

Crepidula argentina, a new species of gastropod of the family Calyptraeidae, is described from the littoral of Mar del Plata, province of Buenos Aires, Argentina. The new species is conchologically similar to *C. protea* d'Orbigny from southern Brazil. *Crepidula argentina* has a larger, subcircular shell and lower convexity than *C. protea*. Anatomical characters that allow differentiation from this latter species are: larger lateral shell muscle and very weak dorsal shell muscle; kidney proportionally smaller, with a characteristic arrangement of inner folds of dorsal lobe; presence of a renal vessel edging rectum and working as adrectal sinus; connection between odontophore muscle pairs m7 and m11; longer salivary gland; four ducts to digestive gland in stomach (instead of two); distinctive arrangement of folds in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland; seminal vesicle of males broad and few coiled; penis and papilla long and narrow; vaginal tube running closely attached to capsule gland. The reproductive biology is also distinctive. *Crepidula argentina* new species has a very well defined seasonal reproductive cycle. Females brood between 1 and 46 egg capsules per spawn. The average total number of embryos per spawn is 5600. The uncleaved, laid egg diameter is 170 µm and the number of eggs per egg capsule is about 320. All eggs develop, there are no nurse eggs. Larvae hatch as planktotrophic veligers. The new species is compared with other members of the genus *Crepidula* from the southern Atlantic coast of South America.

Additional key words: *Crepidula protea*, anatomy, reproduction, littoral.

INTRODUCTION

Most species of mollusks described from the southern Atlantic coast of South America are based on specimens collected by nineteenth century expeditions. *Crepidula* species are no exception. Alcide d'Orbigny (1841) de-

scribed *Crepidula protea* for the first time on his large work "Voyage dans l'Amérique Méridionale". This book was published in several parts in different dates. According to Sherborn and Woodward (1901), Sherborn and Griffin (1934), and Keen (1966) the page (465) with the *C. protea* description (with no illustration) was published on 1841. A year later in the French edition of the Atlas of R. de la Sagra's "Histoire ... de la l'île de Cuba", d'Orbigny published a plate (pl. 24, figs. 30–32) with three illustrations of *C. protea* and no description (A description was published in 1846 in the Spanish edition of the same work.) It seems clear that the intention of d'Orbigny was to publish the chapter of mollusks in Sagra's work before his "Voyage", because he cited that other book despite its later publication. *Crepidula protea* was described without mention of a distinct type locality. A label at The Natural History Museum, London (BMNH) states only "Patagonia" without further geographic details. The examination of the type specimens did not suggest any precise locality nor were there shell characters that could reveal which population they had come from.

D'Orbigny's description and illustration of *Crepidula protea* clearly groups at least two different species. First Dall (1889), and later Hoagland (1977), pointed out that *C. plana* Say, 1822, and *C. unguiformis* Lamarck, 1822, might be included within his concept of *C. protea*. According to d'Orbigny's illustrations and description this seems to be possible.

Parodiz (1939) studied the species of *Crepidula* from Argentina with particular emphasis on the shell and, for the first time, on the radula. Based on a large number of lots from different localities Parodiz described and illustrated the radula and shell of five previously known species and two new subspecies. The subspecies are now considered to be geographical forms. Despite that, Parodiz (1939) is still the most authoritative paper on the genus *Crepidula* from southern Atlantic coast of South

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America. Unfortunately, no anatomical descriptions or reproductive features were described in that work. The specimens examined by Parodiz are still housed at the Museo Argentino de Ciencias Naturales (MACN) and were re-examined in this paper. Since Parodiz's pioneering work no further articles on *Crepidula* from Argentina have been published.

Hoagland (1977) published a comprehensive study of living and fossil species of *Crepidula*. Although her work was basically restricted to North America and the eastern Pacific, she included descriptions and pictures of *C. protea* and *C. dilatata* as well as a few other southern species. Hoagland (1983) described several specimens from Brazil of what she concluded was *C. protea*. She recognized *C. protea* as a species distinct from *C. plana* and *C. unguiformis* and studied d'Orbigny's type material of *C. protea*. In the same paper, Hoagland described the larval development of *C. protea* based on specimens from the southeastern Brazilian coast. Here we consider the specimens she studied to represent actual *C. protea* mainly because they are conchologically similar to the lectotype and paralectotypes.

In an annotated list of several type specimens from the coast of Argentina, Aguirre (1993) designated a lectotype for *C. protea*. Unfortunately, she selected the only complete specimen in d'Orbigny's collection at BMNH. She seems to have been unaware of the differences among the southern species of this genus. Aguirre (1993) mentioned only 4 syntypes when the count is actually 16, arranged in two lots of 5 and 11 specimens respectively (BMNH 1854.12.4.573 and 574) (Hoagland, 1983).

Gallardo (1977, 1979) and Brown and Olivares (1996) described several new species of *Crepidula* from Chile with distinctive reproductive patterns as diagnostic characters. These authors led the way in the search for new characters in this variable genus, showing that in several cases the shell lacks real taxonomic value at the specific level.

Hoagland (1983) and Rios (1985) pointed out that *Crepidula protea* occurs from Rio de Janeiro, Brazil, south to Miramar, in the province of Buenos Aires. However, studies on different population samples along this range revealed that more than one pattern of reproductive strategy and anatomical characters are found, indicating the presence of an unnamed species.

In this paper we describe this new species of *Crepidula* and provide the groundwork for a future revision of the group in the southwestern Atlantic. The new species was originally recognized first by its distinctive reproductive pattern and second through detailed anatomical studies. Comparison with several known species from South America is presented. The study of reproductive biology in the new species is the main topic of another paper (Cledón and Penchaszadeh, submitted.).

MATERIALS AND METHODS

Fresh specimens of *Crepidula argentina* new species used in this study were collected by commercial fish

trawlers at Mar del Plata (38°00' S, 57°33' W) and Puerto Quequén (38°35' S, 58°42' W) along the coast of the province of Buenos Aires, Argentina. Types and material examined are deposited at: Museu Oceanográfico de Rio Grande, Rio Grande do Sul, Brazil (FURG); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN); Museo Nacional de Historia Natural, Montevideo, Uruguay (MHNM); Museu de Zoologia, Universidade de São Paulo (MZSP); National Museum of Natural History, Smithsonian Institution, Washington (USNM). The type material of *C. protea* was studied at The Natural History Museum, London (BMNH).

Specimens were fixed in formalin for at least 24 hours and preserved in 70% ethanol. They were not relaxed. All observations were made on preserved material. Dissections were performed on 3 males and 13 females using standard techniques under a stereomicroscope with the specimens immersed in 70% ethanol. Radulae were prepared (two specimens of *C. argentina* new species of 32.2 and 35 mm length and two of *C. protea* of 18.5 and 17.4 mm) according to the method described by Solem (1972) and observed and illustrated using a LEO 440 scanning electron microscope (SEM) at the National Museum of Natural History, Washington.

Shell measurements including convexity index, were done using the parameters established by Hoagland (1977). Most photographs were taken using a Nikon N70 with a 60 mm Nikkor macro lens. These images were latter scanned from black and white 35 mm negatives using a Nikon Coolscan III slide scanner. All images and plates were processed with the software Photoshop 5.02.

In the figures and text, the following abbreviations are used: **aa**, anterior aorta; **ab**, auricle region beyond ventricle connection; **ac**, anterior extremity of gill on mantle border; **ag**, albumen gland; **an**, anus; **au**, auricle; **bb**, bulged part of br; **bg**, buccal ganglion; **br**, subradular membrane; **bv**, mantle blood vessel inserting in kidney; **cg**, capsule gland; **cv**, ctenidial vein; **da**, aperture of duct to digestive gland; **dd**, duct to digestive gland; **dg**, digestive gland; **dm**, dorsal shell muscle; **dp**, posterior duct to digestive gland; **ea**, esophageal aperture; **en**, endostyle; **es**, esophagus; **fd**, dorsal surface of foot; **fg**, food groove; **fl**, female papilla; **fp**, female pore; **ft**, foot; **gd**, gono-pericardial duct; **gi**, gill; **gs**, gastric shield; **hg**, hypobranchial gland; **in**, intestine; **ir**, insertion of m4 in tissue on radula preceding its exposed (in use) portion; **iu**, U-shaped loop of intestine on pallial roof; **kd**, dorsal lobe of kidney; **ki**, kidney; **kv**, ventral lobe of kidney attached to intestine; **ll**, left lateral expansion (flap) of neck; **lm**, lateral membrane restricting pallial cavity; **m1** to **m14**, odontophore muscles; **mb**, mantle border; **mj**, muscles of jaws and mouth; **ml**, mantle region restricting pallial cavity; **mo**, mouth; **mr**, mantle reinforcement; **mt**, mantle; **nc**, nephrostome; **nr**, nerve ring; **ns**, neck "sole"; **oc**, odontophore cartilage; **os**, osphradium; **ov**, pallial oviduct; **oy**, ovary; **pc**, pericardium; **pd**, penis sperm groove; **pe**, penis; **pg**, pedal gland anterior furrow; **pp**, penis papilla; **pr**, propodium; **pt**, pallial sperm

Table 1. Shell morphometrics of *Crepidula argentina* new species. Linear measurements in mm.

| Specimen # | Total length | Height | Width | Diameter | Septum length | Septum free area | Convexity D/L |
|------------|--------------|--------|-------|----------|---------------|------------------|---------------|
| 1 | 31.5 | 6.3 | 25 | 37 | 13.4 | 17.9 | 1.17 |
| 2 | 35.7 | 7.7 | 24.7 | 41 | 15.1 | 19.8 | 1.14 |
| 3 | 32.8 | 8.6 | 23.1 | 39 | 17.6 | 17.5 | 4.18 |
| 4 | 35.8 | 8.9 | 25 | 42 | 17 | 19.4 | 1.17 |
| 5 | 33.8 | 8.8 | 27 | 43 | 13.7 | 21.8 | 1.27 |
| 6 | 28.1 | 7.1 | 21.7 | 36 | 11.8 | 16.4 | 1.28 |
| 7 | 32.6 | 7.3 | 22.5 | 39 | 13.3 | 17.6 | 1.23 |
| 8 | 30 | 7.3 | 23.4 | 37 | 13.3 | 16.8 | 1.14 |
| 9 | 29.8 | 7.1 | 23.9 | 34 | 12.3 | 16.3 | 1.14 |
| 10 | 33 | 9.3 | 28 | 41 | 14.4 | 19.3 | 1.24 |

groove; **ra**, radula; **rl**, right lateral expansion (flap) of neck; **rn**, radular nucleus; **rs**, radular sac; **sc**, subradular cartilage; **sg**, salivary gland; **sn**, snout-proboscis; **sp**, aperture of *vas deferens* into pallial cavity; **ss**, style sac; **st**, stomach; **sv**, seminal vesicle; **tc**, cephalic tentacle; **tm**, net of transversal muscles of haemocoel; **to**, tissue covering middle region of radula before its exposed part; **ts**, testis; **vc**, visceral connection with haemocoel; **ve**, ventricle; **vg**, vaginal duct; **vm**, visceral mass; **vo**, visceral oviduct; **vs**, vesicles of pallial oviduct.

SYSTEMATICS

Class Gastropoda Cuvier, 1797

Subclass Orthogastropoda Ponder and Lindberg, 1996

Superorder Caenogastropoda Cox, 1960

Order Sorbeoconcha Ponder and Lindberg, 1997

Family Calyptraeidae Lamarck, 1809

Genus *Crepidula* Lamarck, 1799

Crepidula argentina new species

Figures 1–21, 28–46

Crepidula protea: Parodiz, 1939: 702, fig. 8, pl. 1, fig. 6 (not d'Orbigny, 1841).

Diagnosis: *Shell:* Large and wide, slightly convex. Protoconch smooth, with 1¼ whorls. Aperture elliptical. Beak solid, very small. Septum planar, septum margin with sulcus on left side and clear notch in center. Muscle scars absent. Shell externally opaque white, internally white porcelainous. Periostracum absent.

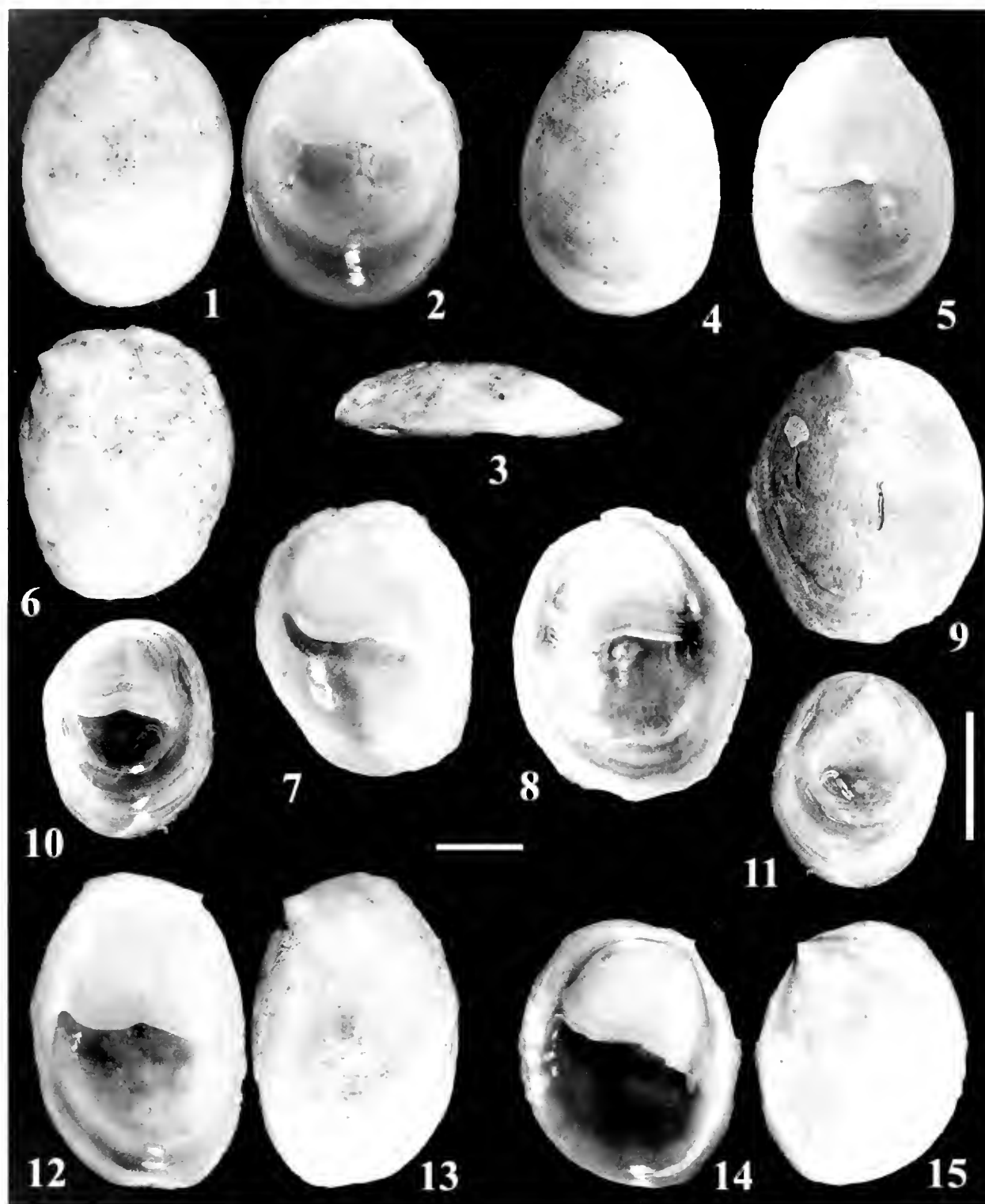
Anatomy: Large lateral shell muscle. Dorsal shell muscle weak. Kidney proportionally small, with characteristic arrangement of inner folds of dorsal lobe, renal vessel edging rectum. Connection between odontophore muscle pairs m7 and m11. Long salivary glands. Four gastric ducts to digestive gland, distinctive arrangement of folds (sorting area) in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland. Seminal vesicle broad and few coiled. Pe-

nis and its apical papilla long and narrow. Vaginal tube running attached to capsule gland.

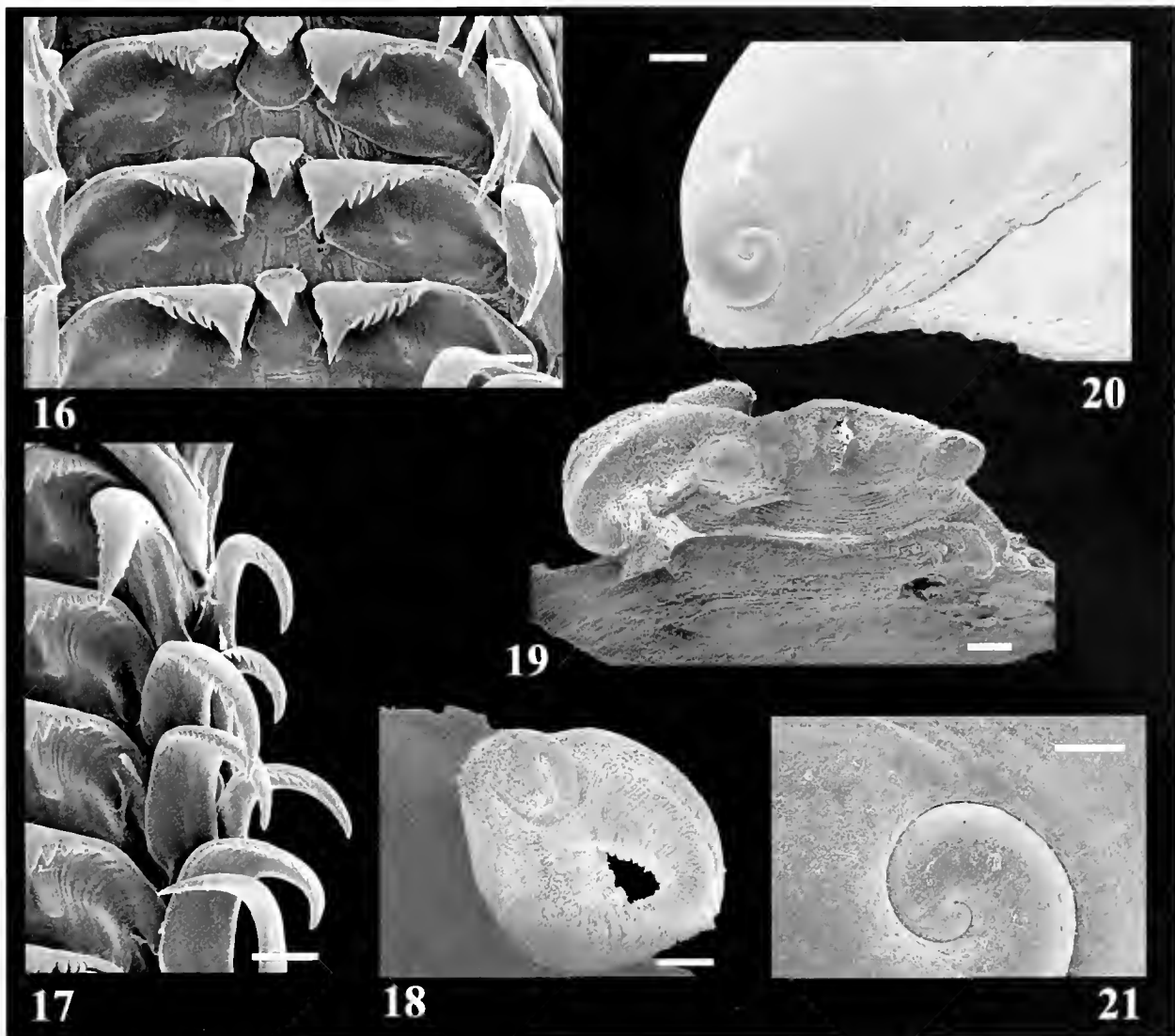
Description: *Shell (Figures 1–15, 20, 21):* Large (np to 40 mm in length) and wide, thin (0.35–0.45 mm in thickness), slightly convex, convexity = 1.20 (see table 1 for other measurements), male specimens very thin, brittle, transparent, planar shells. Protoconch smooth, with 1¼ whorls, transition to teleoconch clearly defined. Aperture elliptical or subcircular. Beak solid, very small, turned to right on females, almost central on males, at level of or only slightly above margin, in males never reaching margin, in females never extended beyond it. Septum planar (never convex), with central ridge almost imperceptible but present, margin of septum with sulcus on left side and clear notch in center, covering less than half of aperture, color bright white with translucent edge. Muscle scars absent. Growth lines covering entire shell. Shell externally opaque-white, internally porcelain-white; some specimens externally with diffuse radial orange lines and/or internally with radial brownish lines. Males always translucent-white externally and bright-white internally. Periostracum absent.

Head-foot (Figures 28, 30, 34, 43): Head protruded, at the end of long (about same length as foot), dorso-ventrally flattened, neck region. Snout short and cylindrical, able to retract and partially invaginate for about half of its length within haemocoelic cavity. Tentacles long, stubby, tip somewhat rounded. Eyes dark, situated on low ommatophores about midway on lateral margin of tentacles. Neck region with pair of lateral, flattened expansions (nuchal lobes); right nuchal lobe bears shallow food groove along its limit with head (figure 28). Sperm groove of males (described below) running externally along food groove (figure 43). Ventral surface of neck region forming an additional, anterior "sole" (figure 30). Foot very ample (occupies about ¾ of shell aperture), dorso-ventrally flattened. Shell septum defining dorsal limit of foot. Mantle fusing with dorsal surface of foot and protruding beyond its borders. Furrow of pedal glands transversal, located on central region of anterior margin of foot (about 1/3 of its width); a small, pointed expansion present on each side of furrow (figure 30). Anterior margin of foot covering ventrally posterior region of neck "sole". Columellar muscle very reduced, small flap contouring anterior border of shell septum, only evident on right side. Inner haemocoelic cavity narrow, running approximately along center of neck region, almost entirely filled by mass of salivary glands (described below) and numerous, transversal, very slender muscle fibers (figure 34); these fibers connect ventral surface of dorsal haemocoelic wall with dorsal surface of its ventral wall.

Mantle organs (Figures 29, 31–33, 44): Mantle border very thick, edging entire ventral margin of shell, free on its anterior half and attached to foot edge on its posterior half. Mantle border without appendages, but entirely covered by a series of minute glands. Mantle border with



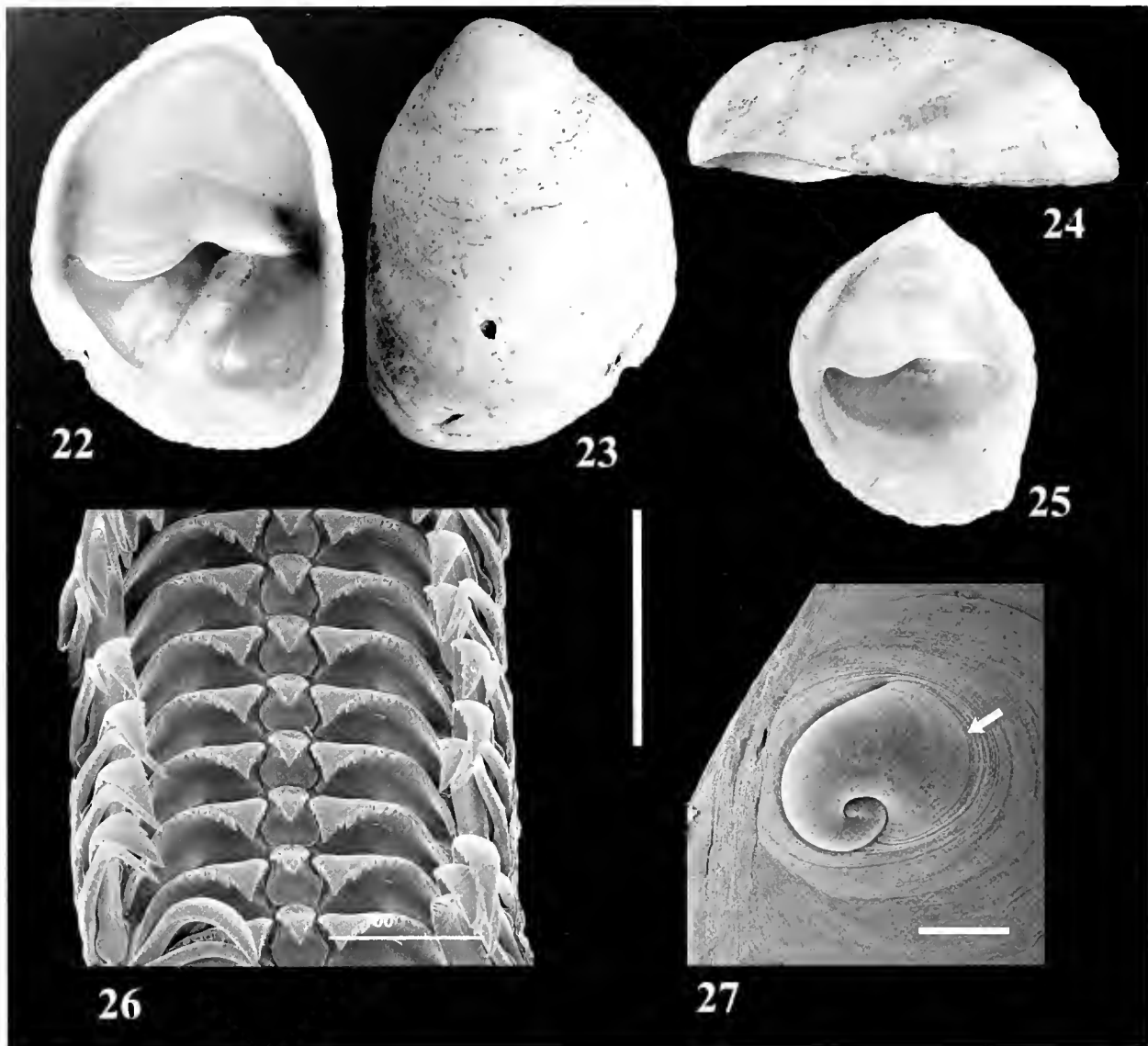
Figures 1–15. Shells of *Crepidula argentina* new species. 1–3. Holotype, MACN 34508, Mar del Plata, Buenos Aires, Argentina. 4–5. Paratype, MACN 34509, Mar del Plata, Buenos Aires, Argentina. 6–7. Paratype, MACN 34509, Puerto Quequén, Buenos Aires, Argentina. 8–9. Paratype. 10–11. Paratype, MACN 34509, male specimen, scale bar on right side of figure 11 = 0.5 mm (for figures 10 and 11). 12–13. Paratype, MACN 34509. 14–15. Paratype, MACN 34509. Scale bar under figure 5 = 1 cm for all specimens, except figures 10 and 11.



Figures 16–21. *Crepidula argentina* new species. **16–17.** Radula. **16.** Radula, frontal view. Scale bar = 30 µm. **17.** Radula, marginal teeth, scale bar = 30 µm. **18–19.** Penis, critical-point dried. **18.** Dorsal view. Scale bar = 200 µm. **19.** Ventral view. Scale bar = 200 µm. **20–21.** Protoconch. **20.** Dorsal view. Scale bar = 300 µm. **21.** Detail of figure 20. Scale bar = 100 µm.

characteristic arrangement of folds along central region of aperture of pallial cavity (figure 33), a broad furrow beginning on anterior extremity of gill, running toward left side, and ending at about right third of osphradium; this thick fold presents broad central furrow. Dorsal shell muscle apparently lacking in most specimens, very reduced and difficult to observe in others (figure 29). Lateral shell muscle well developed, inserting broadly in left lateral region of mantle border and region posterior to it, originating shortly in inner shell surface in region close to left anterior edge of shell septum. Pallial cavity aperture occupying about 2/3 of anterior half of shell border, turned to right (drawing an analogy between shell in dorsal view and a clock, with head occupying 12:00, pallial aperture occupies a sector beginning at 9:00 and ending at 2:00). Pallial cavity deep, broad, triangular, arched and flattened dorso-ventrally (figure 29).

Anterior extremity of pallial cavity slightly larger than its aperture due to constriction on left and right extremities produced by fusion of mantle and foot (figures 31, 44). Pallial cavity narrows gradually in posterior direction, penetrating left side of visceral mass (described below); cavity length about 3/4 of total length of animal. Osphradium (figure 33) long, monopectinate, located between anterior region of gill and mantle border, occupying about middle region of pallial aperture, somewhat perpendicular to longitudinal axis of animal, compressed between gill and mantle border. Osphradium length slightly exceeding 1/5 of pallial aperture length. Osphradium leaflets long, somewhat thick, closely packed, with rounded tip. Gill very large, with somewhat narrow base, edging anterior and left margin of pallial cavity along almost its entire length; anterior extremity of gill in anterior and left region of pallial cavity aperture, near its

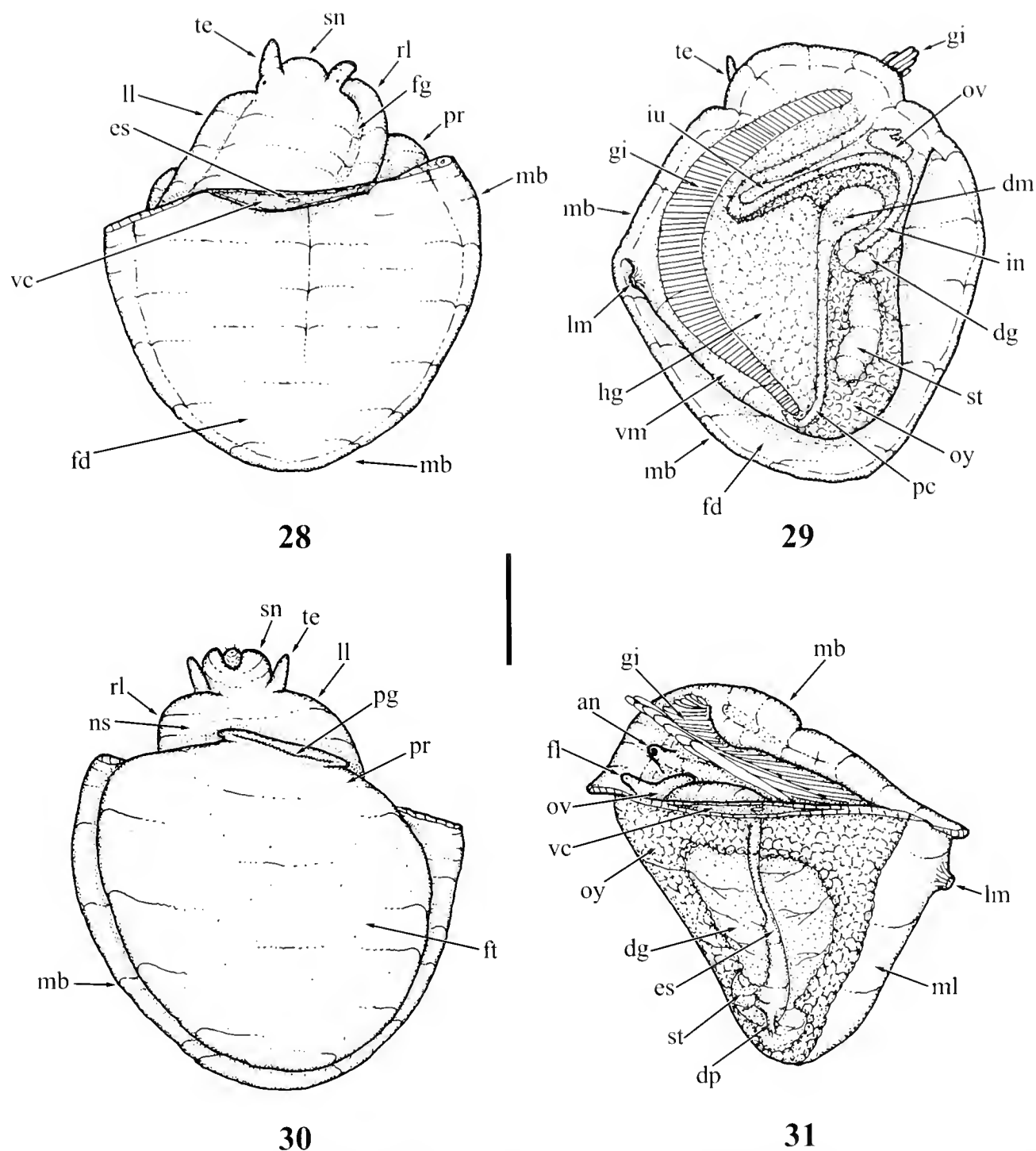


Figures 22–27. *Crepidula protea* d'Orbigny, 1841. **22–24.** Shell, MACN 34511, off Ubatuba, São Paulo, Brazil, 23°30' S, 44°54' W, 42 m, dorsal, ventral, and lateral views of the same specimen. **25.** Shell, MACN 34511, other specimen in lot, ventral view. Scale bar = 1 cm for all shells. **26.** Radula, frontal view. Scale bar = 100 μ m. **27.** Protoconch, dorsal view. Scale bar = 300 μ m.

right limit, on thick mantle border; posterior extremity of gill in posterior end of pallial cavity (figure 32). Base of gill filaments triangular. Gill filament with very long, almost straight, stiff rod extending to right; rods extend for about twice as long as their triangular, membranous base; these rods begin in region of ctenidial, in left margin of cavity roof, touching food groove of head-foot, in right margin of cavity floor. Rod apex rounded and preceded by a thicker region. Gill filaments connected to each other by cilia, mainly along their thicker apical region, which helps maintain somewhat gill structure. Gill filaments longer in central region of gill, shortening gradually toward both extremities. Anterior extremity of gill with short filaments, abruptly turning forwards, ending at mantle border (figure 33). Ctenidial vein cylin-

drical. Endostyle well developed, yellowish (a somewhat narrow glandular ridge located on ventral surface of ctenidial vein and present along its entire length) (figure 33). Hypobranchial gland whitish, low, slightly developed, occupying surface between gill and visceral mass (figures 1, 5). About 1/3 of visceral mass encroaches on pallial cavity roof, occupying about 1/3 of posterior and right sectors of this region; pericardium and kidney located in posterior part; long intestinal loop, anus, and pallial oviduct in anterior part (described below).

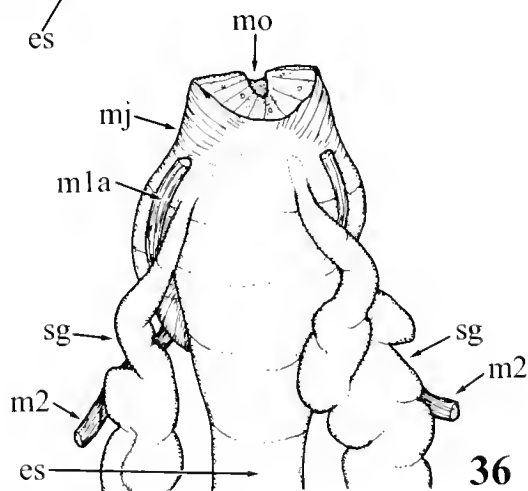
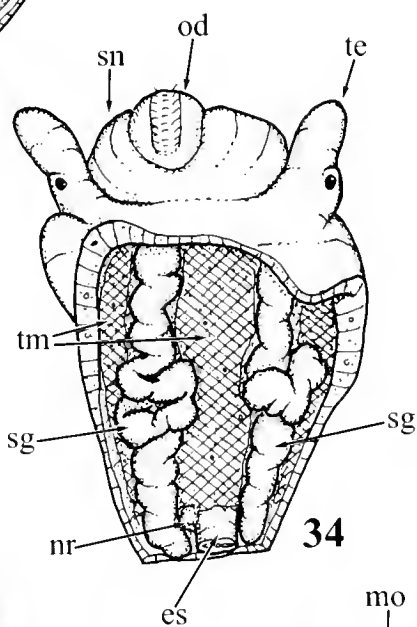
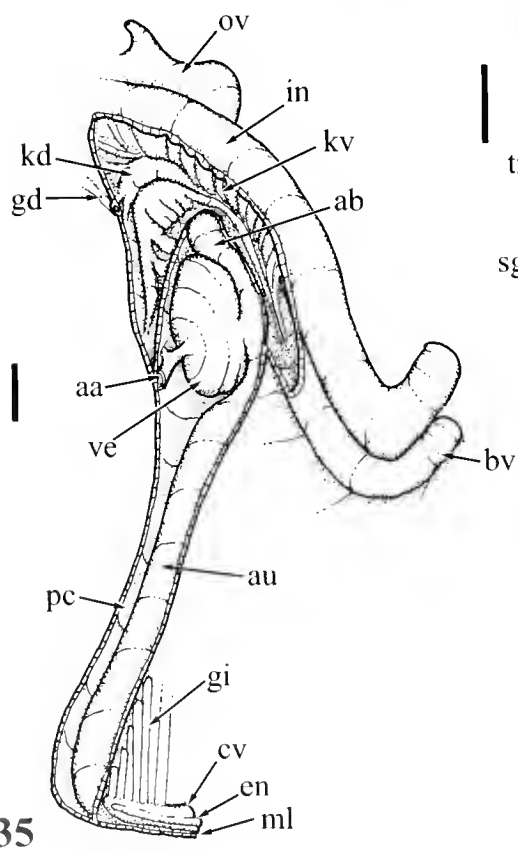
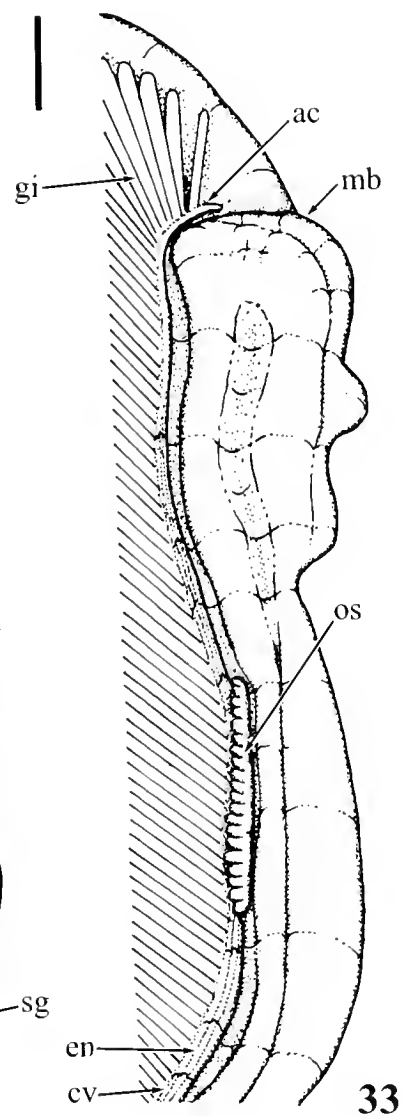
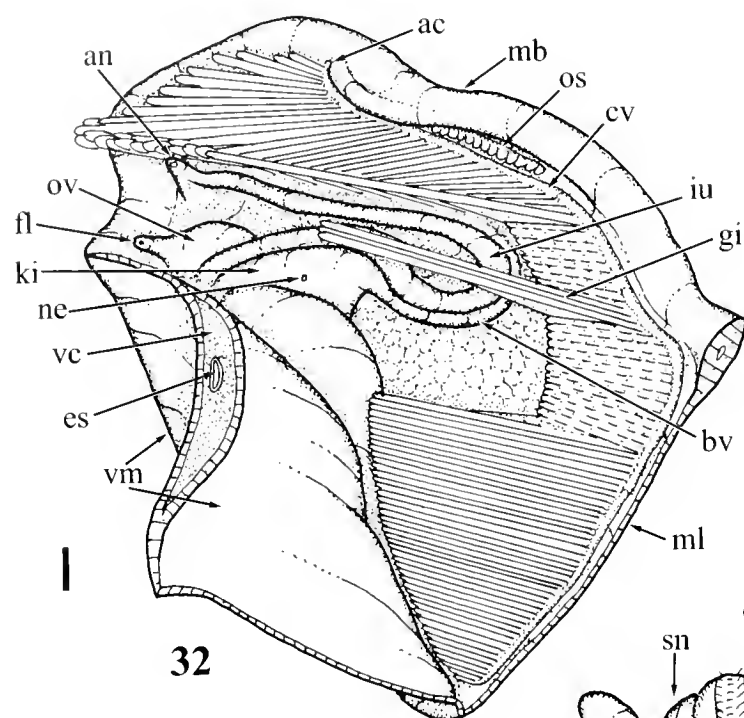
Visceral mass (Figures 29, 31, 32, 44): A dorso-ventrally flattened cone lying in shell chamber produced by septum. Thin calcareous septum separating visceral mass from dorsal surface of foot. Left and anterior region of



Figures 28–31. Anatomy of *Crepidula argentina* new species. **28.** Female animal with shell, visceral mass, and pallial cavity removed, dorsal view. **29.** Same animal, whole, dorsal view. **30.** Same, ventral view. **31.** Isolated visceral mass and pallial cavity, ventral view. Scale bar = 5 mm.

visceral mass occupied by pallial cavity (figures 31, 44). Remaining region of visceral mass with stomach as central structure, immediately and almost completely surrounded by digestive gland (except in some ventral and dorsal parts). Gonad surrounding digestive gland externally.

Visceral mass encroaching on right and posterior regions of pallial cavity roof. Anterior extremity of visceral mass (ventral to posterior pallial cavity region) covering columellar muscle just posterior to anterior border of shell septum.



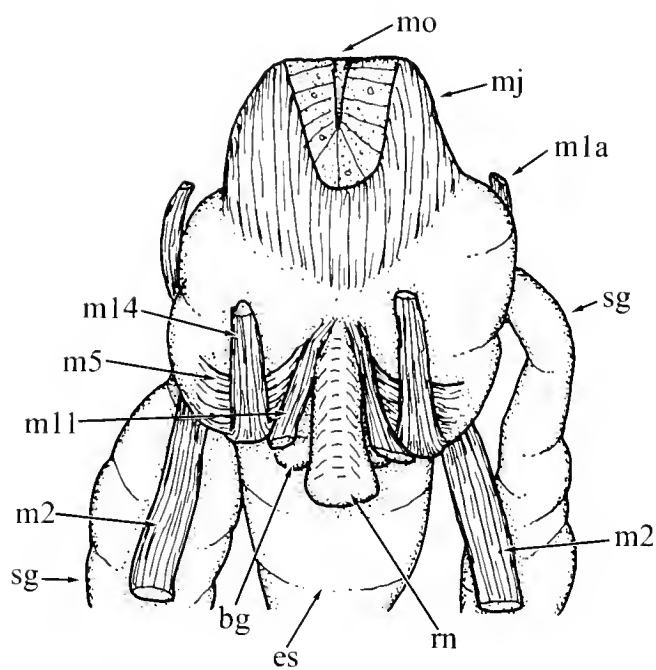
Circulatory and excretory systems (Figures 29, 35): Pericardium very long, somewhat perpendicular to longitudinal axis of animal (figure 29); very narrow in posterior extremity of gill (posterior and left end of pallial cavity); running along anterior margin of visceral mass where it encroaches on pallial roof, enlarging gradually and ending at about middle level of this region of visceral mass, near its median line. Pericardium circumscribes (1) pallial cavity in anterior and ventral direction, (2) visceral mass (mostly gonad) in posterior direction, (3) mantle in dorsal direction, and (4) kidney to right. Auricle thin-walled and very long, running long entire pericardium length, attached to its anterior and dorsal inner surfaces; auricle connects with ventricle approximately along its middle and right thirds; auricle portion beyond connection with ventricle represented by broad blind sac. Ventricle elliptical, very muscular, its connection with auricle located about middle region of its anterior surface; aortas originating in opposite side. Anterior aorta broad, directed away from posterior aorta. Anterior aorta directed toward right, edging posterior inner surface of pericardium. Anterior aorta penetrates head haemocoel. Kidney small, occupying about 1/4 of area of visceral mass when projected on inner surface of pallial cavity. Kidney circumscribes (1) mantle in dorsal direction, (2) pallial cavity in ventral and left lateral direction, (3) visceral mass (mostly gonad) in posterior and right direction, (4) pericardium in posterior and left direction, (5) an intestinal loop in anterior direction, (6) intestine and oviduct (when present) in lateral right direction. Kidney mostly hollow, with pair of very irregularly shaped lobes. Ventral lobe with several, slight narrow transverse folds attached to posterior surface of adjacent intestine. Dorsal lobe occupies most of dorsal and lateral surfaces, bearing several irregular folds in left direction; part of lobe covering ventral surface around nephrostome. Nephridial gland thin, present along boundary between kidney and pericardium, bearing series of transverse, narrow folds connected with dorsal renal lobe. Nephrostome a very small slit in left region of ventral wall. A broad vessel connected with left extremity of kidney and running along external pallial loop of intestine for about 3/4 of its length.

Digestive system (Figures 29, 31, 32, 34–42): Mouth longitudinal, in center of anterior surface of snout (figure 34). Buccal mass very large, occupying most of inner space of snout. Buccal mass capable of some protraction and invagination. Dorsal wall of buccal mass with pair of broad and thin jaw plates. Pair of dorsal folds broad and low, connected to jaws in posterior direction. Odon-

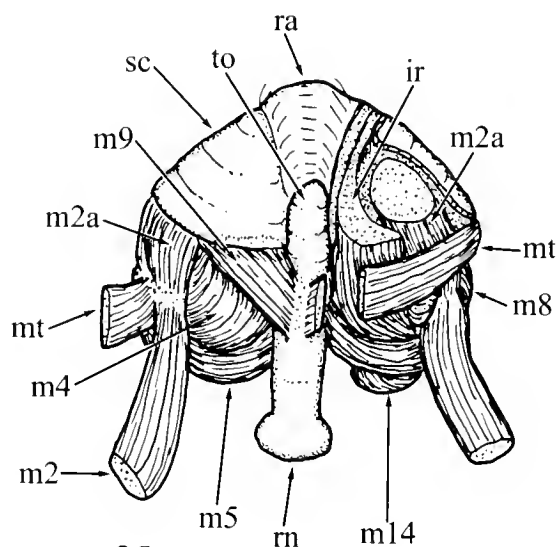
tophore large, consisting of most of volume of buccal mass. Odontophore muscles (figures 36–38, 40, 41): (m1) jugal muscles, several very narrow muscles connecting buccal mass to adjacent wall of snout, more concentrated anteriorly around mouth; (m1a) pair of dorsal protractor muscles, narrow, thin and superficial, with origin in antero-dorsal region of mouth, close to its median line, insertion in postero-dorsal and lateral region of odontophore; (mj) jaws and peribuccal muscles, somewhat thick, surrounding lateral and dorsal wall of buccal mass, with origin around mouth, insertion in middle region of lateral and dorsal wall of odontophore; (m2) pair of retractor muscles of buccal mass (retractor of pharynx), broad, with origin in latero-ventral region of haemocoel just posterior to snout, running in anterior direction, with insertion in postero-lateral and dorsal region of odontophore cartilages; (m2a) pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, running in anterior direction, with insertion in subradular cartilage in middle region of its dorsal inner surface; (mt) dorsal transversal muscle or ventral approximator muscle of cartilages, connecting dorsally posterior-dorsal and lateral surface of both cartilages, lying between superficial membrane that covers odontophore and tissue on middle region of radula (to); (m4) pair of median dorsal tensor muscles of radula, very large and thick, with origin in ventral-central and posterior region of odontophore cartilages, running along their middle region, contouring meso-ventral surface of cartilages, running along their dorsal surface, with insertion in dorsal-posterior and medial extremity of subradular cartilage; (m5f) pair of median radular tensor muscles, thick, with origin in meso-posterior and dorsal regions of odontophore cartilages, just adjacent to m2 insertion and m2a origin, crossing middle region of m4, running toward medial region of m4, with insertion along radular sac on both sides (each branch of m5 runs along a side of radular sac, medially and dorsally); (m6) horizontal muscle, very thin, uniting anterior half of odontophore cartilages, with insertion on their dorsal margin; (m7) pair of ventral tensor muscles of radula, thin and narrow, with origin in meso-anterior margin of m4, running in posterior direction adjacent to subradular membrane, bifurcating in posterior region of odontophore, median branch connecting with that of other member of pair and inserted in meso-posterior region of radular sac, lateral branch connecting with m11; (m8) pair of strong muscles with origin in postero-dorsal and lateral region of odontophore cartilages just adjacent to insertion of m2, running along and attached to dorsal margin of odontophore car-

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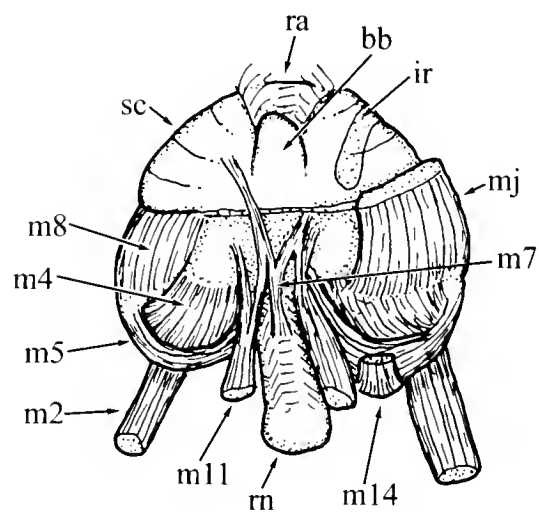
Figures 32–36. Anatomy of *Crepidula argentina* new species. **32.** Pallial cavity, ventral view, part of visceral mass deflected, some gill filaments of central part of gill removed. **33.** Detail of mantle border and pallial cavity at anterior extremity of gill. **34.** Head and haemocoel, ventral view, foot and neck “sole” removed. **35.** Detail of visceral mass at border of pallial cavity, adjacent to pericardial structures, ventral view, ventral surface of pericardium and kidney membranes removed. **36.** Buccal mass, dorsal view. All scale bars = 1 mm.



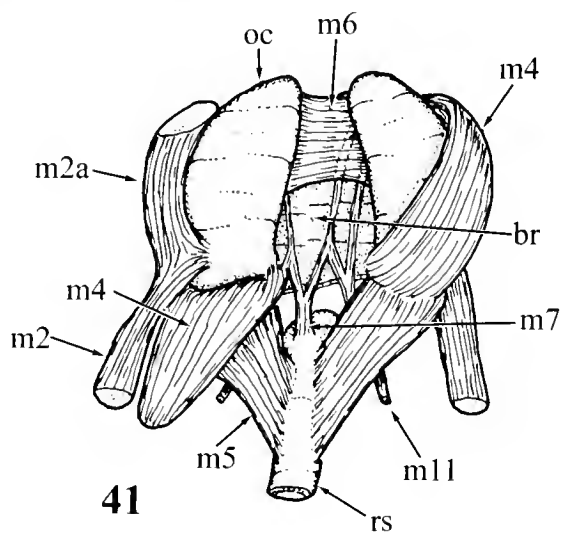
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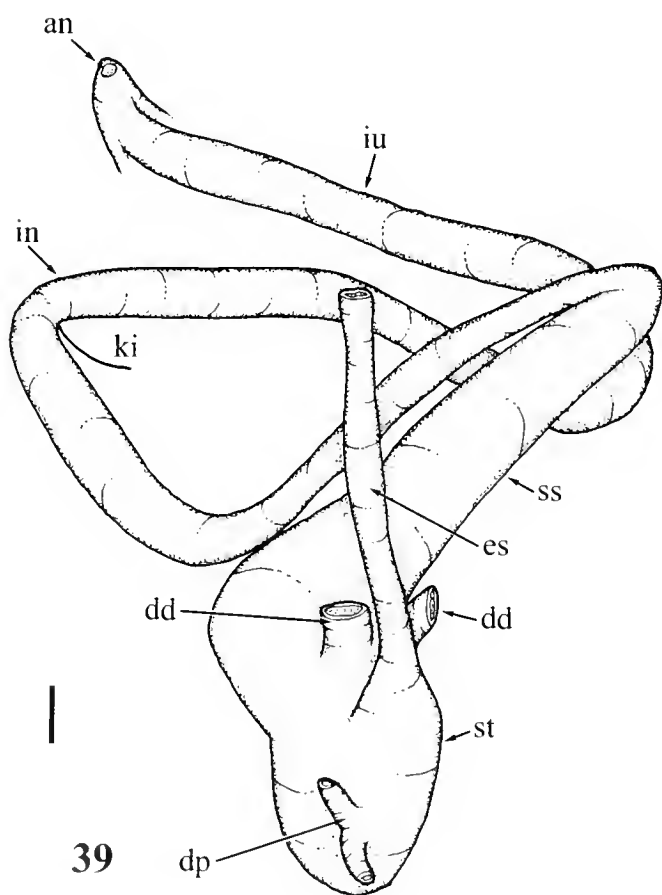
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tilages, with insertion in their antero-dorsal region adjacent to horizontal muscle (m6); (m9) pair of dorso-medial tensor muscle of radula, broad and thin, with origin along meso-dorsal surface of radular sac (in its region internal to odontophore), crossing to dorsal surface, with insertion in dorso-ventral margin of subradular cartilage; (m11) small, narrow pair of muscles, with origin in meso-ventral region of mouth, running in posterior direction along its median line, penetrating in median region of odontophore, running between m7 and m4, with insertion in anterior region of subradular membrane; (m14) pair of broad and thin muscles, with origin in postero-dorsal region of odontophore, close to origins of m2 and m5, running in antero-ventral direction, with insertion in inner ventral surface of snout at about middle region of odontophore; to) tissue covering middle region of radula within odontophore, along its dorsal surface; br) subradular membrane, covering ventral surface of subradular cartilage and some neighboring areas.

Radula taenioglossate, short, measuring little more than odontophore length (figures 37, 38). Rachidian tooth tall, narrow with curved, convex base, central cusp very large and sharp, at least two weak denticles on each side decreasing in size toward lateral teeth, no basal cusps but pair of lateral reinforcements present along borders. Lateral tooth broad (about 3 times rachidian width), curved inward, with conspicuous apical cusp turned toward rachidian line and 5–7 short, triangular denticles along edge on marginal side and 2–3 very weak denticles on edge on rachidian side, denticles decreasing in size in both directions, disappearing at about middle region of tooth, only a thickened border remaining. Marginal teeth long, curved, tall, tip sharply pointed, with serrate inner margin (at least 7 denticles); inner marginal tooth broad, about twice as wide as outer marginal tooth.

Pair of buccal ganglia large, close together near median line (figure 37), situated between buccal mass and adjacent esophagus. Salivary glands very long, tubular, coiled (about 3 times longer than haemocoel length when straightened) (figure 34). Several narrow transverse muscles unite internally dorsal and ventral surfaces of haemocoel, passing both sides of salivary glands, esophagus, and aorta (figure 34). Salivary glands not passing through nerve ring. Ducts of salivary glands thick, running to dorsal surface of buccal mass, penetrating adjacent wall of buccal mass; apertures small, close to site of penetration, located in anterior region of dorsal folds of buccal mass (figure 36).

Esophagus narrow and long (figure 39). Inner surface of anterior esophagus with a pair of broad folds. Middle

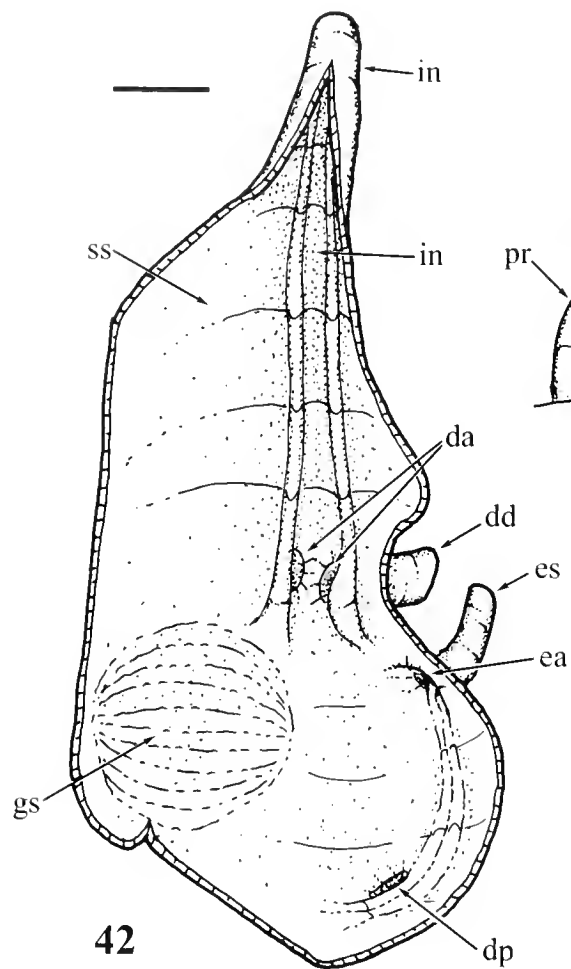
esophagus with pair of narrow folds (continuation from those of anterior esophagus) and moderately spacious glandular chamber. Inner surface of posterior esophagus with 4–5 longitudinal, narrow, folds of similar dimensions. Stomach (figures 39, 42) large, slightly conical, occupying about half of visceral mass; esophagus inserting in left side of its posterior region of stomach, adjacent to region of shell apex. Four ducts to digestive gland present: anterior pair narrow, inserted in ventral surface, between insertion of esophagus and posterior gastric end, one turned in anterior direction and other to opposite side; posterior pair of ducts thick, located in middle region of ventral and left surface of stomach, one at considerable distance from other. Stomach gradually narrows in anterior and left direction, close to left and posterior extremity of pallial cavity. Stomach inner surface (figure 42) with pair of narrow and long folds, both with origin adjacent to insertion of esophagus, lining posterior surface of stomach, gradually disappearing in direction posterior to apertures of anterior ducts to digestive gland. Gastric shield thin, presenting transversal folds marking a somewhat elliptical, concave area. Anterior half of stomach with a pair of slight tall, longitudinal folds; posterior region between both folds smaller than anterior region; smaller region as intestinal branch of stomach; broader (anterior) region as style sac. Digestive gland pale-brown in color, surrounding stomach except for some spots in dorsal and ventral surfaces.

Intestine very narrow and sinuous (figure 39); running from left to right adjacent to anterior border of stomach, running up near median line to right and anterior extremity of visceral mass; in this region and toward left, it surrounds right and anterior border of kidney, turning suddenly to right and running parallel to preceding loop; both loops exposed along pallial roof (figures 29, 32, 35, 39). Anus small, slightly siphoned, situated in right region of pallial cavity close to mantle border (figures 31, 32, 39). Last loops of intestine contain numerous, small, somewhat elliptical fecal pellets.

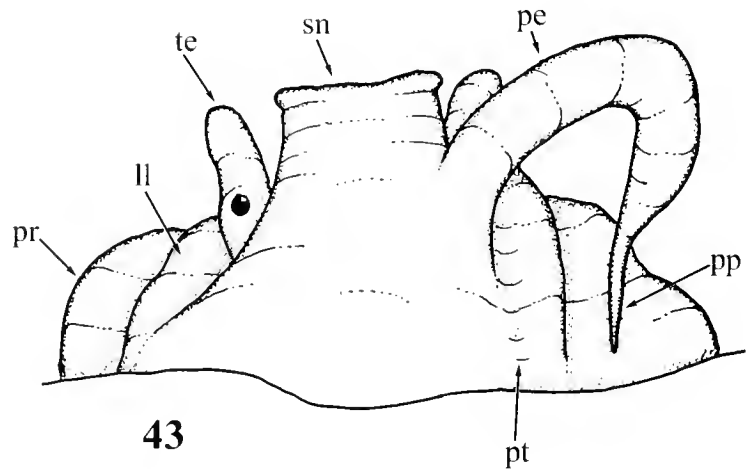
Male genital system (Figures 43, 44, 46): Only small specimens (up to 9 mm) are functional males. Testis situated in anterior region of visceral mass, color orange. Seminal vesicle convoluted, very thickened, color cream, situated in anterior and right region of visceral mass, where it abruptly narrows, becoming very slender and opening in postero-ventral and right region of pallial cavity. A shallow groove runs from this aperture to penis base, on pallial floor near right margin of head. Sperm groove better defined and deeper in anterior direction. Penis long (about 3 times tentacle length), curved, orig-

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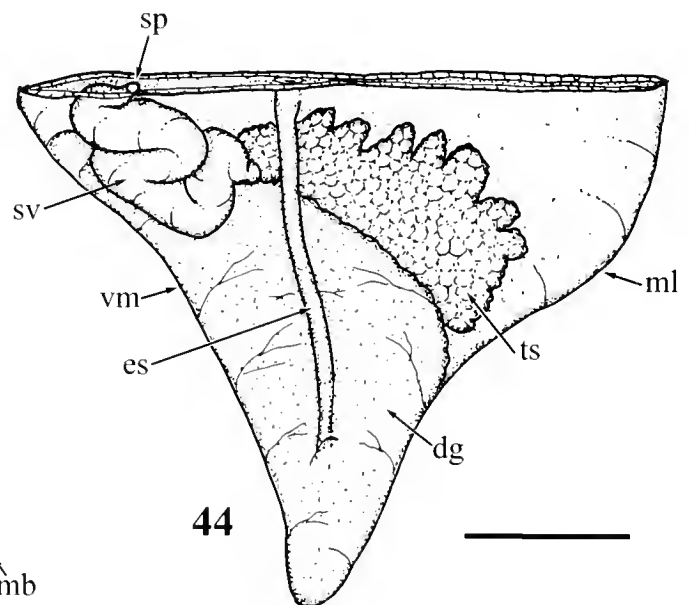
Figures 37–41. Anatomy of *Crepidula argentina* new species. **37.** Buccal mass, ventral view. **38.** Odontophore, dorsal view, some muscles sectioned and deflected, part of right region of subradular cartilage removed to show muscular insertions in it. **39.** Digestive tubes seen *in situ* with visceral mass as a transparent structure, ventral view. **40.** Odontophore, ventral view, superficial membrane and muscles removed, right mj (left in figure) also removed. **41.** Odontophore, ventral view, radular sac deflected and only partially shown, odontophore cartilages deflected from each other, right m4 (left in figure) deflected downward. All scale bars = 1 mm.



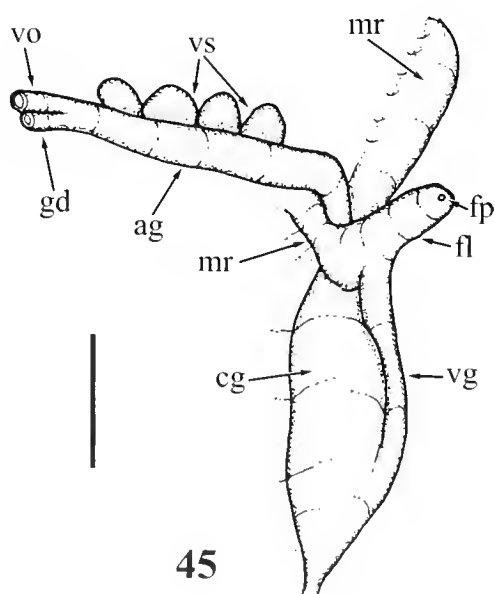
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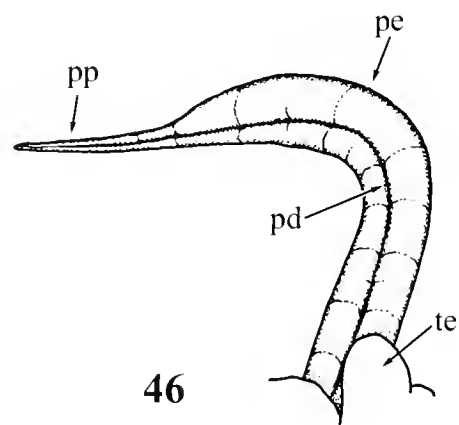
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inating dorsally to right tentacle. Papilla on penis tip, very long, about half of penis length. Penis duct opened, running along middle region of ventral surface of penis to tip of papilla.

Female genital system (Figures 29, 31, 32, 35, 45): Ovary pale brown, surrounding digestive gland, denser in anterior region of visceral mass (figures 29, 31). Visceral oviduct very narrow, running from left to right in anterior border of visceral mass. Gonopericardial duct well developed, slightly thicker than visceral oviduct, with origin in ventral and right extremity of pericardium (figure 35); running along visceral glands encroached in pallial cavity; inserted in posterior extremity of pallial oviduct where it joins insertion of visceral oviduct. Albumen gland long, moderately thick, whitish; walls thick, glandular; situated in anterior and right extremity of visceral mass; 3 to 4 seminal receptacles inserted along right surface of albumen gland. Capsule gland a continuation of albumen gland, marked by sudden increase of secretory tissue in wall and by turn toward left; walls irregular, thick, glandular. Vaginal tube moderately narrow, originating in posterior region of capsule gland, running attached to this latter up to its right limit, where it abruptly turns in ventral direction to form tall genital papilla. Papilla with pair of low folds running along its posterior side, from base almost to tip; folds close to each other with narrow furrow in between. Female genital pore situated in tip of papilla (figures 31, 32, 45) slit-like, transversal, with posterior and anterior edges slightly projected.

Etymology: The specific epithet, a noun in apposition, refers to the name of the country where the species occurs, Argentina.

Type locality: Mar del Plata, Buenos Aires, Argentina in 35–50 m, on shells of *Mytilus edulis platensis* d'Orbigny, 1846.

Type material: Holotype, MACN 34508; 20 paratypes, MACN 34509 (10 dry specimens) and MACN 34510 (10 specimens preserved in ethanol); 6 paratypes, MLP 5578; 16 paratypes (3 males, 13 females) MZSP 32152; 6 paratypes USNM 2016009 (1 specimen preserved in ethanol); MHNH, 6 specimens without number; 6 paratypes MHNH 15105; all from type locality.

Additional material examined: MACN 18504, 39 specimens, Puerto Quequén, Buenos Aires; MACN 8887, 9 specimens, off Mar del Plata, in 46 m; MACN 11367, 36 specimens; MACN 9361–49, 5 specimens; MACN 18374, 2 specimens; MACN 8653, 4 specimens; MACN 11586, 27 specimens; all from Mar del Plata; MACN 20529–1 more than 60 specimens, mouth of Rio Negro.

Literature records: Due to similarities with *C. protea*, most literature records should be re-checked from now on. Records cited by Parodiz (1939) were revised and are included in the material examined.

Distribution: Province of Buenos Aires, Argentina, from Mar del Plata to the mouth of Rio Negro, on banks of *Mytilus edulis platensis*, 35–50 m depth. Records from Uruguay and Brazil need to be confirmed.

Reproductive pattern: *Crepidula argentina* new species is a protandrous hermaphrodite that undergoes complete sex change. Males mature at about 4 mm length. Sex change begins when individuals reach approximately 9 mm and is completed when the first previtelogenic oocytes appear, usually at around 11 mm length. The smallest brooding female we found was 15.0 mm length and the largest 39.0 mm.

The new species has a well-defined seasonal reproductive cycle. Between September and March more than 30% of the females are brooding, with maximum brooding in January (57%). In June and July brooding is uncommon (0–10%). Females brood 1–46 egg capsules per spawn. The average number of embryos per spawn is 5600. There is no correlation between size of the female and number of egg capsules or eggs per spawn. However, female size, capsule size, and the average number of embryos per capsule are positively correlated (Cledón and Penchaszadeh, submitted). Uncleaved egg diameter is 170 μm and there are about 320 eggs per egg capsule. All eggs develop, there are no nurse eggs, and the only extra-embryonic nutritional source is the intracapsular liquid. There is no record of cannibalism in early or advanced stages of development. The embryos hatch as planktotrophic veliger larvae.

DISCUSSION

Crepidula argentina new species is usually found on the posterior edge of living shells of *Mytilus edulis platensis* d'Orbigny, 1846, typically in association with *Calyptraothes garthi* (Fenucci, 1975) (Crustacea: Brachyura). Mytilid banks, distributed all around the coast of Argentina (Penchaszadeh, 1971a) are a suitable habitat for *Crepidula argentina*.

Crepidula argentina was included by different authors (Parodiz, 1939; Hoagland, 1977; 1983, in part) in *C. protea* and referred to as *C. unguiformis* by Penchaszadeh (1971b: 480). The type specimens of *C. protea* were examined by Hoagland (1983). At BMNH, there are two lots with 5 and 11 syntypes under the numbers 1854.12.4.573 and 574 respectively. Aguirre (1993) designated and illustrated the only whole specimen as lectotype plus two paralectotypes, with no mention to

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Figures 42–46. Anatomy of *Crepidula argentina* new species. **42.** Stomach, ventral view, inner surface exposed by means of a longitudinal incision. **43.** Head of male, dorsal view. **44.** Visceral mass and adjacent part of pallial cavity, male, ventral view; **45.** Pallial oviduct, ventral view. **46.** Penis, ventral view. All scale bars = 1 mm.

Hoagland's paper or d'Orbigny's (in Sagra) illustrations. Most of the type specimens are smaller than 30 mm and have the conchological attributes of what Hoagland described for *C. protea* from Brazil. In terms of shell characters, *C. protea* and *C. argentina* new species are similar. Measurements of *C. argentina* in Table 1 are identical to those given to *C. protea* by Hoagland (1977). However, in a later paper, Hoagland (1983) mentioned that the largest specimen of *C. protea* was 20 mm long. Therefore, we suspect that both species were combined under the name *C. protea* in her 1977 paper. *Crepidula argentina* is larger and wider, particularly in young specimens. *Crepidula protea* has an elliptical aperture with a thicker and more convex shell, while the new species has a subcircular aperture and a thinner and flatter shell. Both species differ primarily in their anatomical features and reproductive strategy. Further anatomical study of *C. protea* is provided in another paper (Simone, submitted); some data from that paper are here discussed for comparative purposes. *Crepidula argentina* differs morphologically from *C. protea* in that *C. argentina* has: 1) a more developed lateral shell muscle, 2) a poorly developed dorsal shell muscle, 3) the kidney proportionally smaller and with a different arrangement of inner folds of dorsal lobe, 4) presence of a renal vessel edging rectum and working as adrectal sinus, 5) a connection between odontophore muscle pairs m7 and m11, 6) a longer salivary gland, 7) four ducts to digestive gland in stomach, instead of two, 8) different arrangement of folds in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland, 9) seminal vesicles of males broader and less coiled, 10) penis and papilla longer and narrower, and 11) vaginal tube running closely attached to capsule gland.

Embryological features of *Crepidula argentina* are very distinct from those of *C. protea* (fide Hoagland, 1983). The total number of embryos per spawn and per egg capsule and the size range of brooding females are the most remarkable differences. Furthermore, Hoagland (1986) described later stages of developing embryos (veliger stage) as pinkish in color and embedded in a sticky gelatinous matrix in which the embryos did not move freely. We never observed this in pre-hatching stages of *C. argentina*.

It is possible to differentiate several species of *Crepidula* along the southern Atlantic coast of South America. Parodiz (1939) cited five species of *Crepidula* for the Argentine coasts: *C. dilatata* Lamarck; *C. aculeata* (Gmelin); *C. protea* d'Orbigny; *C. onyx* Sowerby and *C. unguiformis* Lamarck. Specimens of *Crepidula unguiformis* were described by Parodiz as usually associated with hermit crabs. The distribution of *C. unguiformis* is given by Hoagland (1977) as restricted to the Mediterranean Sea and Northern Africa. It is probable that "*C. unguiformis*" *sensu* Parodiz is a distinct, perhaps unnamed, species. *Crepidula onyx* from the northern Pacific was cited by Parodiz (1939) as living in northern Patagonia. However, Hoagland (1977) based on Parodiz's drawing of the radula of *C. onyx* presumed that "*C.*

onyx" *sensu* Parodiz is a different species: *C. aplysioides* Reeve, 1859. The latter species was cited as a synonym of *C. onyx* by Parodiz (1939). Hoagland (1977) described *C. aplysioides* as a different species ranging from Grenada south to Brazil and Argentina. Reeve's types were not examined. This type material includes four specimens and is housed at the BMNH (Reg. Number: 1977137). As far as we know, there is no species similar to *C. aplysioides* Reeve on the coast of Argentina.

The study of the family Calyptraeidae and the genus *Crepidula* in particular is less than finished for the region in study. It is expected that additional new species will be detected and described following detailed studies on anatomy and reproductive biology of these mollusks.

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Three new species of the genus *Merica* (Neogastropoda: Cancellariidae) from South Africa and the Philippines

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ABSTRACT

Three new species of the cancellariid genus *Merica* are described: *Merica lussii* from South Africa, and *M. deynzeri* and *M. ektypophos* from the southern Philippines. The South African *Merica lussii* has previously been misidentified in the literature as *Cancellaria bifasciata* Deshayes, 1830, a junior subjective synonym of *C. oblonga* Sowerby, 1825, from which it differs in having a broader, stepped spire, a proportionally shorter but broader aperture, and a deeply impressed sutural canal. *Merica deynzeri* differs from other Philippine species of *Merica* by its deeply impressed sutural canal, its much stronger and coarser axial and spiral sculpture, more rounded aperture, and its lack of banding pattern. *Merica ektypophos* can be distinguished from all other described species of *Merica* in its distinctively heavy, inflated shell, as well as by its extremely coarse axial and spiral sculpture.

Additional key words: Gastropoda, Caenogastropoda, Recent, western Pacific.

INTRODUCTION

Merica was originally proposed as a subgenus of *Cancellaria* by H. and A. Adams (1854: 277) to distinguish those species with reticulate sculpture, oblique columellar folds and an internally lirate outer lip, but lacking a prominent emargination or notch on the outer lip at the base of the siphonal canal. This taxon has been accorded generic status in most twentieth century works (e.g., Habe, 1961; Petit, 1974; Noda, 1980; Verhecken, 1986a, 1986b), while retained as a subgenus of *Cancellaria* in several faunistic surveys (e.g., Springsteen and Leobrera, 1986; Wilson, 1994; Higo *et al.*, 1999). *Merica* has been reported from the later Tertiary of Europe (Cossmann, 1899; Sacco, 1904; Janssen, 1984) and the Indo-Pacific region (Shuto, 1969; Noda, 1908; Ladd, 1982). In the Recent fauna, *Merica* appears limited to the Indo-West Pacific, ranging from South Africa, along

the northern Indian Ocean, through Indonesia to Australia and northward to Japan, usually at sublittoral depths. As pointed out by Verhecken (1986a: 38–40), there is considerable confusion in the literature as to the correct nomenclature for many of the currently recognized species of *Merica*.

This paper describes three new Recent species of *Merica*, one from South Africa and two from the Philippines. The assignment of *Cancellaria oblonga* Sowerby, 1825, to the genus *Merica* is reaffirmed, and the species is illustrated for comparative purposes. Holotypes of the new species are housed in the collections of the Natal Museum (NM), Pietermaritzburg, Republic of South Africa, and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851

Subfamily Cancellariinae Forbes and Hanley, 1851

Genus *Merica* H. and A. Adams, 1854

Merica H. and A. Adams, 1854:277. Type species: *Cancellaria melanostoma* Sowerby, 1849, by subsequent designation of Cossmann, 1899.

Diagnosis: Shell with conical spire, large body whorl, paucispiral protoconch weakly to strongly deflected from teleoconch axis, prominent suture, generally weak siphonal fasciole, narrow pseudo-umbilicus, and large, ovate aperture. Columella short, thick, weakly concave, with 2 sharply keeled columellar folds and strong siphonal fold. Columellar lip with pustules and secondary folds. Parietal callus generally present. Emargination along outer lip at base of siphonal canal poorly defined or absent.

Remarks: *Merica* appears to be the Indo-Pacific stem group for the genus *Cancellaria*, which is limited to the eastern Pacific and the western Atlantic. *Merica* differs in lacking a pronounced emargination along the outer lip of the shell as well as a heavy, bifurcated posterior

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columellar fold, both characteristic of *Cancellaria*. Cossmann (1899: 13) accorded generic status to *Merica*, and most authors have followed this.

Kuroda and Habe (1971: 310, 202) proposed the genus *Momochora* based primarily on the presence of a strongly deviated protoconch in its type species, *Cancellaria sinensis* Reeve, 1856. *Momochora* has been considered a synonym of *Merica* by most subsequent authors (Garrard, 1975: 3; Verhecken, 1986a: 44).

Merica oblonga (Sowerby, 1825)

(Figures 1, 5, 6)

Cancellaria oblonga Sowerby, 1825: Appendix: 15; 1832: fig. 19.

Cancellaria bifasciata Deshayes, 1830: 181; Löbbecke, 1855: 30, pl. 9, figs. 1, 2.

Cancellaria oblonga Sowerby: Kiener, 1841: 6, pl. 3, fig. 3; Abbott and Dance, 1982: 225; Springsteen and Leobrera, 1986: 78, pl. 18, fig. 26.

Cancellaria (Merica) oblonga Kiener [sic]: Chenu, 1859: 277, fig. 1847.

Not *Cancellaria (Merica) bifasciata* Deshayes: Chenu, 1858: 277, fig. 1845 [= *M. sinensis* (Reeve, 1856)].

Not *Cancellaria bifasciata* Deshayes: Barnard, 1959: 13–14; Kensley, 1973: 194, fig. 749 [= *M. lussii* new species].

Merica bifasciata (Deshayes): Habe, 1961: pl. 24, fig. 27.

Cancellaria (Merica) bifasciata Deshayes: Oyama and Takemura, 1963: *Cancellaria* plate, fig. 6.

Merica oblonga (Sowerby): Petit, 1974: 112, fig. 5; Verhecken, 1986a: 41, figs. 7–8; Verhecken and Wranik, 1991: 60; Verhecken, 1997: 308, fig. 37.

Momochora bifasciata (Deshayes): Higo, 1973: 179.

Momochora oblonga (Sowerby): Higo and Goto, 1993: 276; Higo *et al.*, 1999: 294.

Remarks: For many years there was confusion about priority of the names applied to this species, with *Cancellaria bifasciata* Deshayes, 1830, generally given precedence over *Cancellaria oblonga* Sowerby, 1825. These two available names were correctly dated by Petit (1974). *Merica oblonga* (as *Merica bifasciata*) was attributed to the genus *Momochora* by Higo (1973:179), and this placement remained unchanged in the two later revisions and enlargements of that work (Higo and Goto, 1993; Higo *et al.*, 1999). As *M. oblonga* has a protoconch that is not strongly deflected from the coiling axis of the teleoconch (Figs. 5,6), we see little justification for the usage of *Momochora*.

There were, and to a lesser degree still remain, questions about the geographic range of this species. Its occurrence in Panama, as reported by Kiener (1841), was shown to be incorrect by Keen (1971:649). Verhecken (1997:309) gave the distribution of *Merica oblonga* as "Japan to Indonesia; Northern Indian Ocean to Aden; Eastern South Africa (?)." His query regarding the South African records is appropriate, as the South African specimens previously identified as *Merica bifasciata* represent a new species, described herein as *Merica lussii*.

There are no verifiable Japanese records for *Merica oblonga* (Kazunori Hasegawa, personal communication).

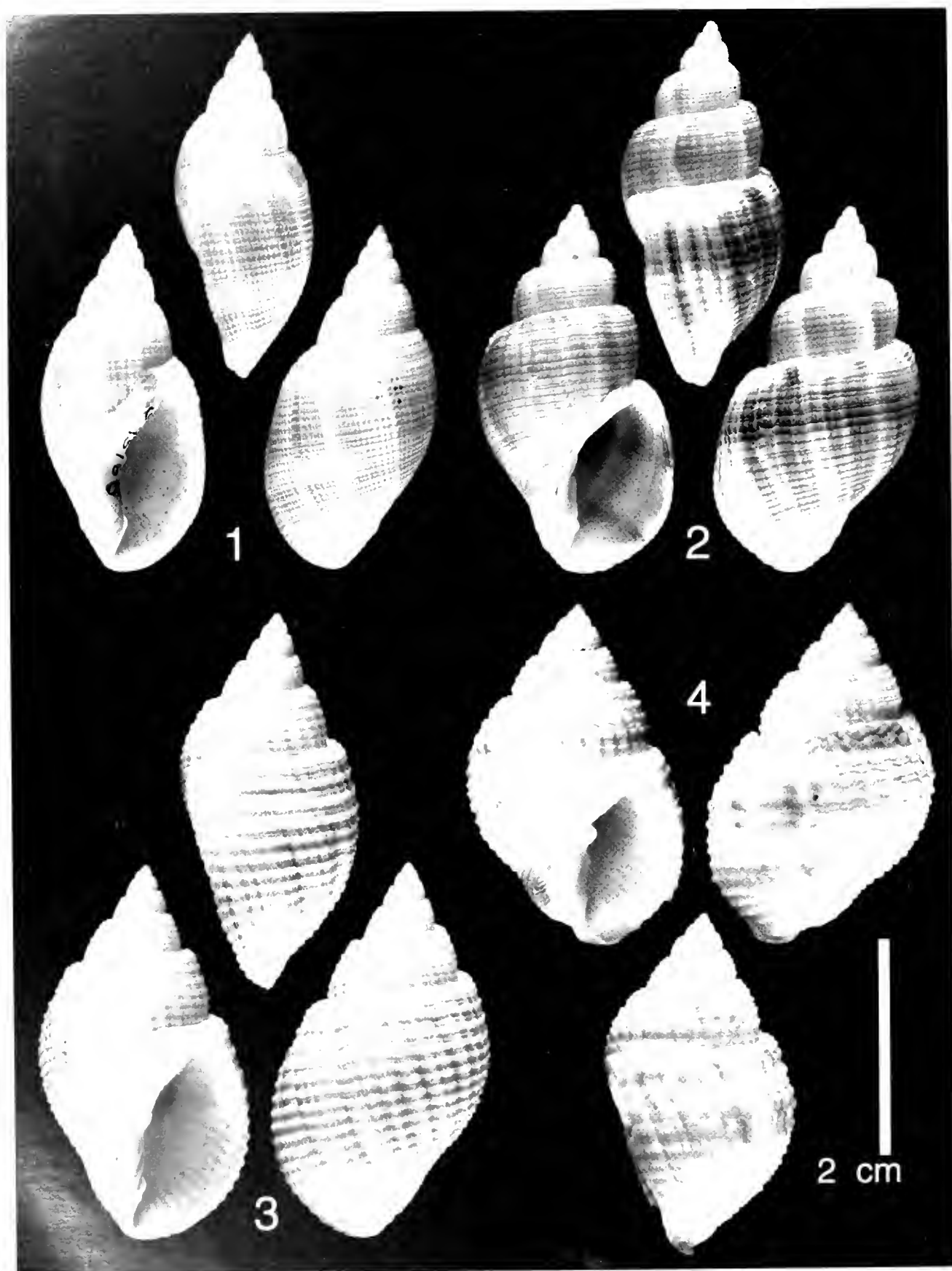
The figure of *M. oblonga* published by Habe (1961) and reproduced by Petit (1974) is of a specimen from Taiwan that was included by Habe for comparison with *Merica asprella* [sic] Lamarck. The specimen figured by Oyama and Takemura (1963) is also from Taiwan. Verhecken's (1986a: 41) record for Japan is based on Habe's usage. Records of *M. oblonga* are noticeably absent in most standard Japanese compendia and lists. Its inclusion in the exhaustive faunal lists of Higo (1973), Higo and Goto (1993) and Higo, Callomon and Goto (1999) was based on a Japanese publication of uncertain authorship.

Merica oblonga ranges as far north as Taiwan. It is uncommon in the Philippines. Springsteen and Leobrera (1986: 78) record this species as "sporadically found throughout the Philippines in limited quantity." The color figure in Abbott and Dance (1982:225) is of a Philippine specimen taken from over 30 m depth in tangle nets (Petit collection). Verhecken and Wranik (1991: 60) state that *M. oblonga* "seems to have its distribution center in the eastern Indian Ocean (Gulf of Bengal)." While this species is uncommon in other areas, it appears to be common in India. We have seen commercial lots from India containing hundreds of specimens of *M. oblonga*.

Merica lussii new species

(Figures 2, 7, 8)

Description: Shell (figure 2) to 35 mm, thin, biconic, elongate. Spire high (spire angle 53–55°) comprising one-half of total shell length. Protoconch (figures 7, 8) paucispiral, nearly coaxial with teleoconch (deviated from coiling axis by up to 4°), increasing in diameter from 300 µm to 2.15 mm in 2½ elongated whorls. Transition to teleoconch marked by onset of spiral then axial sculpture. Teleoconch of about 5 evenly rounded whorls. Shoulder rounded. Suture broadly impressed, forming conspicuous canal. Axial sculpture of 30–34 very weak, rounded, slightly prosocline ribs, as broad as intervening spaces. Axial ribs become prominent, irregular, crowded on final ¼ of body whorl. Spiral sculpture more pronounced than axial, of regularly spaced, flat, primary cords (8–10 on penultimate whorl, 25–32 on body whorl) with weaker secondary cords present irregularly, but most often on posterior portion of whorls. Aperture large, broadly ovate, deflected from coiling axis by 16–17°. Outer lip thin, weakly flared outwardly, without discernible emargination. Inner lip smooth or with weak spiral lirae reflecting spiral cords, especially in the anterior portion. Inner lip with 2 columellar, 1 siphonal fold. Siphonal fold flat, bifid on holotype but sharp on other specimens. Columellar lip thick, forming inductural shield that obscures chink-like umbilicus. Siphonal canal short, broad, inconspicuous. Base color light yellow-brown, irregularly marked with white and various shades or reddish brown. Two bands of brown sometimes present, visible inside aperture. Wider band just below shoulder, narrower band just posterior to base of



siphonal canal. Axial flammules of brown, yellow, white, irregular in outline and intensity.

Type locality: Off Park Rynie, about 80 km S of Durban, on the KwaZulu-Natal south coast, South Africa, approximately 30°17' S, 30°45' E, dredged in 150 m on rubble and sponge substrate.

Type material: Holotype, NM V7648/T1312, height 34.4 mm; Paratype 1, Marcus Lussi Collection, both from the type locality; Paratype 2, Dawn Brink Collection, near type locality in 140 m, rubble and sponge bottom; Paratype 3, NM E8794, Zululand, off Matigulu River mouth, 29°21.4' S, 31°56.5' E, in 145 m, mud, shell rubble, NMDP 16 Apr 1989, station ZR7.

Etymology: Named for Mr. Markus Lussi of Durban North, South Africa, who has made numerous contributions to the literature on South African Mollusca, and who provided specimens for study.

Comparative remarks: *Merica lussii* differs from *M. oblonga* in having a broader shell with a stepped spire, a proportionally shorter but broader aperture, and a deeply impressed sutural canal. *Merica lussii* lacks the closely packed strong axial ribs that produce the finely beaded surface characteristic of *M. oblonga*. Barnard (1959: 14) and Verhecken (1986a: 42) have previously suggested that South African records of *M. bifasciata* (= *M. oblonga*) might represent a distinct species.

Merica deynzeri new species
(Figures 3, 9, 10)

Description: Shell (figure 3) to 35 mm, thick, biconic, weakly pseudo-umbilicate. Spire high (spire angle 55–58°). Protoconch (figures 9, 10) paucispiral, deviated from coiling axis by about 14°, increasing in diameter from 300 µm to 2.15 mm in 2¼ evenly rounded, glassy whorls. Transition to teleoconch marked by onset of spiral cords followed almost immediately by axial ribs. Teleoconch of up to 6 whorls. Shoulder inconspicuous. Suture deeply impressed, forming narrow canal. Axial sculpture of 27–33 low, evenly spaced, prosocline ribs, rounded in profile, as wide as intervening spaces. Periodic internal varices (see Harasewych and Petit, 1982: 111) barely discernable on outer surface of shell by thickened axial rib slightly expanded along edge of sutural canal followed closely by thin axial rib and slightly reflected lip, begin after about 2½ whorls, continue at intervals of about 240° thereafter. Spiral sculpture of strong, broad cords (20–26 on body whorl, 8–9 on pen-

ultimate whorl) that are narrower, more closely spaced near suture and siphon. Spiral cords overlay axial ribs to produce a cancellate surface on early whorls. Single, secondary cords occur between primary cords along central region of whorls. Axial ribs become progressively broader, irregular, more widely spaced on last half of body whorl, obscuring cancellate appearance. Aperture large, broad, nearly hemi-elliptical, deflected from coiling axis by 14–15°. Outer lip weakly recurved in profile, with finely serrated edge, lacking emargination. Inner surface of outer lip with 16 recessed spiral lirae that diminish 1/3 whorl into the aperture. Inner lip with 2 columellar, 1 siphonal fold, columellar lip nearly covering pseudo-umbilicus. Posterior columellar fold strongest, overlying weak siphonal fasciole. Anterior columellar fold extends to edge of columellar lip. Spiral ridge parallels anterior columellar fold adapically, but is confined to the columellar lip without extending into aperture. Surface of siphonal fold with single pustule in some specimens. Siphonal canal short, narrow, axial. Color uniform yellow-brown, sometimes with narrow darker bands above and below mid-whorl. Portions of spire whorls indicate that juveniles may be mottled.

Type locality: Off Balicasag Island, Bohol, Philippines. Taken in tangle nets at approximately 200 meters.

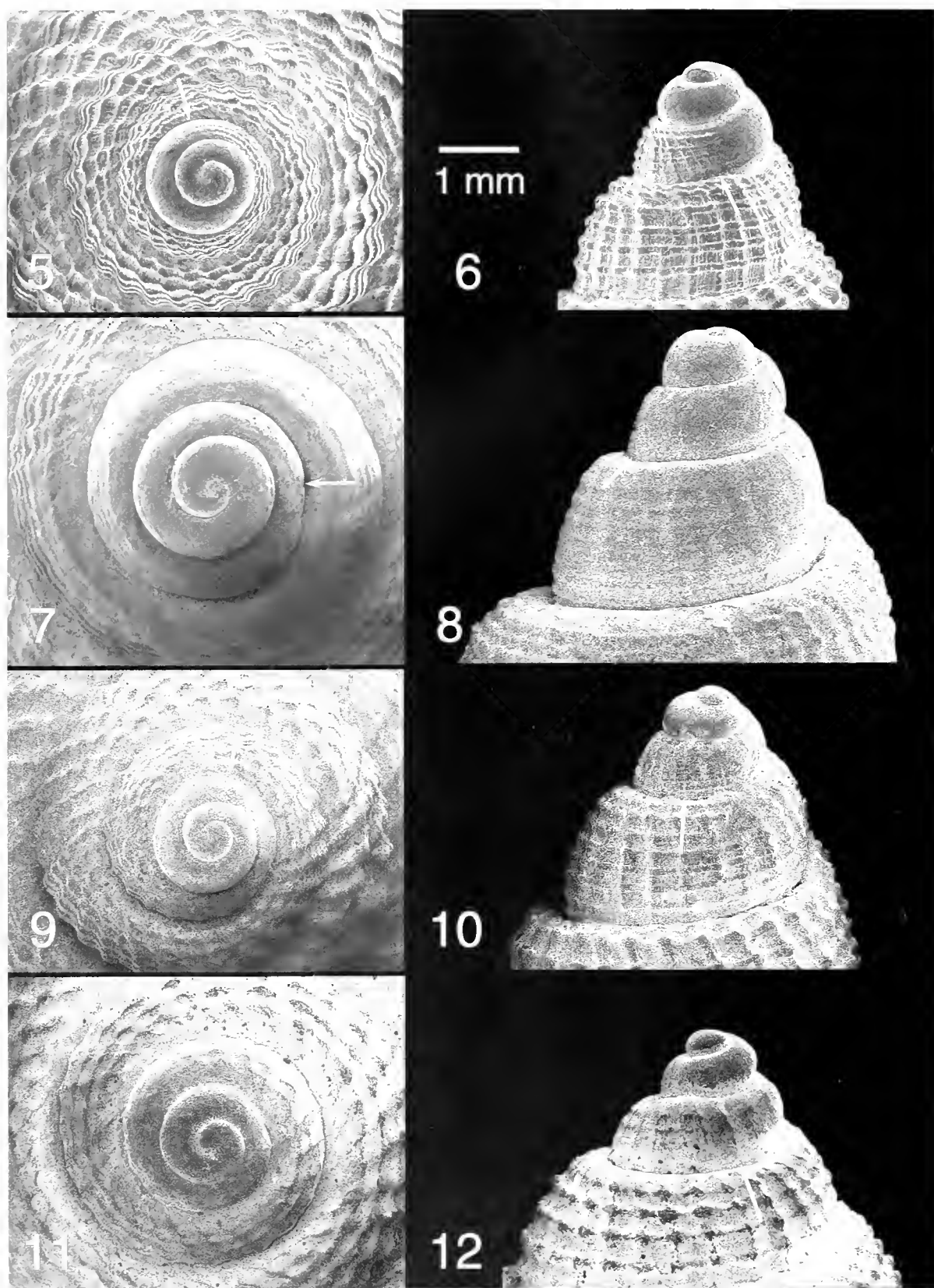
Type material: Holotype, USNM 880645, height 35.2 mm; Paratype 1, R. Petit Collection 2465, both from the type locality; Paratypes 2–4, USNM 242316, off Pt. Dumurug, Masbate, Philippines (12°00'30" N, 124°05'36" E), dredged in 280 m, green mud, USFS Albatross, sta. 5394, 13 Mar 1909; Paratypes 5–8, USNM 242321, off Adyagan Island, E Masbate, Philippines (12°12'35" N, 124°02'48" E), dredged in 247 m, green mud, sand, USFS Albatross, sta. 5392, 13 Mar 1909; Paratype 9, USNM 277485, off Sibugay Island, E of Masbate, Philippines (12°04'15" N, 124°04'36" E) in 198 m, gray sand, mud, 15.5°C, USFS Albatross, sta. 5212, 20 Apr 1908.

Etymology: We take pleasure in naming this species for Mr. Al Deynzer of Sanibel, Florida, who obtained these and other uncommon Cancellariidae in the Philippines and made them available for study.

Comparative remarks: This new species is distinctive in having a well-developed sutural margin strongly rounded to form a deeply impressed sutural canal. *Merica deynzeri* is similar to, but stockier and broader than *M. oblonga*, from which it can also be distinguished by its much stronger and coarser axial and spiral sculpture, and by its more rounded aperture. A notable feature of

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Figures 1–4. Apertural, lateral and dorsal views of the shells of: 1. *Merica oblonga* (Sowerby, 1825), USNM 845168, taken by fishing trawler in Manila Bay, Luzon, Philippines, 1969. 2. *Merica lussii* new species, holotype, NM V7648/T1312, off Park Rynie, about 80 km south of Durban on the KwaZulu-Natal south coast, South Africa, approximately 30°17' S, 30°45' E, dredged in 150 meters, rubble and sponge substrate. 3. *Merica deynzeri* new species, holotype, USNM 880645, off Balicasag Island, Bohol, Philippines, taken in tangle nets from about 200 meters. 4. *Merica ektiphos* new species, holotype, USNM 880646, Off Balicasag Island, Bohol, Philippines, taken in tangle nets from about 200 meters. Scale bar = 2 cm for all figures.



Figures 5–12. Scanning Electron Micrographs of axial and lateral aspects of protoconchs of specimens in figures 1–4: 5–6, *Merica oblonga* Sowerby, 1825; 7–8, *Merica lusu* new species; 9–10, *Merica dopuzeri* new species; 11–12, *Merica ektiphos* new species. Arrowheads indicate transition from protoconch to teleconch. Scale bar = 1 mm for all figures.

Merica deynzeri is the lack of color bands that are characteristic of most species of *Merica*.

Merica ektyphos new species
(Figures 4, 11, 12)

Description: Shell (figure 4) to 33 mm, very thick, globose, pseudo-umbilicate. Spire relatively low (spire angle 63°). Protoconch (figures 11, 12) paucispiral, deviated from coiling axis by about 8°, increasing in diameter from 400 μ m to 2.10 mm in 2½ low, evenly rounded whorls. Transition to teleoconch marked by onset of axial ribs followed by overlying spiral cords. Teleoconch of up to 6 rounded whorls. Suture impressed, forming deep, narrow sutural canal. Axial sculpture of prominent, prosocline ribs (31 on body whorl, 31 on penultimate whorl). Ribs become smaller, more densely spaced in narrow bands spaced every ½ to ¾ whorl, indicating position of internal varices. Spiral sculpture of strong, flattened cords (15–16 on body whorl, 6 on penultimate whorl) that form nodes at intersections with axial ribs. Nodes especially pronounced at margin of sutural canal, forming serrated ridge. Finer secondary threads present between adjacent cords above suture line. Aperture large, deflected from coiling axis by 12°, with broadly elliptical outer lip, sharp, 48° angle between columella and parietal wall. Outer lip prosocline, slightly crenate, with 12–13 strong, slightly recessed lirae that become reduced, disappearing about ¼ whorl within the aperture. Outer lip with emargination discernible only by touch as shallow depression. Columella with 2 columellar, 1 siphonal fold. Posteriormost fold strongest, overlying conspicuous siphonal fasciole, does not reach edge of columellar lip as anterior and siphonal folds do. Columellar lip thick, rounded, nearly covering pseudo-umbilicus. Four weak, short spiral ridges run along columellar lip parallel to and posterior to anterior columellar fold, but do not extend into aperture. Siphonal canal short, narrow, well demarcated, deflected from axis. Color whitish, with ginger brown bands along suture (darkest), above mid-whorl (broadest), below mid-whorl (narrowest) and along siphonal fasciole. Gaps in coloration of sutural band correlate with internal varices.

Type locality: Off Balicasag Island, Bohol, Philippines. Taken in tangle nets at approximately 200 meters.

Type material: Holotype, USNM 880646, 32.3 mm; Paratypes 1–4, R. Petit Collection 2472; Paratypes 5–7, Deynzer Collection, all from type locality.

Etymology: Gr. *ektyphos*, puffed up. Named for its inflated shell.

Comparative remarks: This new species can be distinguished from all known species of *Merica* by the thickness of its shell and the strength of its sculpture. In outline it is closest to the Australian *M. westralis* (Garrard, 1975), from which it differs in having much coarser axial and spiral sculpture, a straighter columella with

Table 1. *Merica deynzeri* new species. Measurements of shell characters. Linear measurements in mm. n = 5. ° n = 3 for no. whorls, protoconch.

| Character | Mean | SD | Range |
|-------------------------|-------|-------|-------------|
| Shell length (SL) | 35.0 | 2.6 | 34.9–35.6 |
| Aperture length (AL) | 22.1 | 1.7 | 19.6–24.3 |
| AL/SL | 0.629 | 0.003 | 0.624–0.632 |
| No. whorls, protoconch° | 2.5 | 0 | 2.5–2.5 |
| No. whorls, teleoconch | 5.53 | 0.14 | 5.33–5.67 |
| Spire angle | 56.7° | 1.3° | 55–58° |

stronger folds, and a body whorl that is much less constricted behind the siphonal fasciole.

ACKNOWLEDGMENTS

We thank Marcus Lussi and Dawn Brink of South Africa for making specimens of *Merica lussii* available for this study. While on visits to the Philippines Al Deynzer made special efforts to obtain specimens for this study. We are grateful to Paul Callomon of Osaka and Dr. Kazunori Hasegawa of Ibaraki for information about the Japanese records of *M. oblonga*.

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Systematics of the genus *Infundibulum* Montfort, 1810 (Gastropoda: Trochidae)

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Two Recent *Infundibulum* species are recognized: *I. concavum* (Gmelin, 1791) (type species) and *I. tomlini* (Fulton, 1930). Their shells are convergent on those of calyptraeid limpets of the genus *Trochita* Schumacher, 1817, having the most widely excavated bases and the most strongly tangential apertures of any living Trochini. They live firmly attached to rocks on highly exposed shores from low tide level to several meters depth in tropical seas. Reliable records of *I. concavum* are from Réunion and Mauritius. All Recent specimens of *I. tomlini* seen were from old collections, and most have either minimal, often dubious locality data, or none at all, though it would seem that *I. tomlini* has a patchy distribution in the tropical southwest Pacific.

Additional key words: Mollusca, Trochoidea, fossils, Pleistocene, Kermadec Islands.

INTRODUCTION

The present contribution was initiated some years ago when I recognized a species of *Infundibulum* among Pleistocene fossils from Raoul Island, Kermadec Islands, northeast of New Zealand. A search of the literature revealed that *Infundibulum* species are surprisingly poorly known. Moreover, inquiries revealed that most of the few specimens of *Infundibulum* species in museum collections were acquired during the nineteenth century, and have broad, often dubious locality data, or none at all. The fossils from Raoul Island prove to be the little known species *I. tomlini* (Fulton, 1930), which is represented in old collections labeled as originating variously from Penang (Pinang, Malaysia), Australia, Upolu (Western Samoa), Lifou (Loyalty Islands) or the New Hebrides (Vanuatu). Of these locality records, only Upolu, Lifou, and Vanuatu seem likely to be correct. Museum specimens of the type species (*Trochus concavus* Gmelin, 1791) are labeled as having originated from localities in the Indian Ocean, as well as the Red Sea and Cochin China (southern Vietnam), though the only reliably localized specimens seen during the present study

were from Réunion. An explanation for the poor representation of *I. concavum* (and presumably *I. tomlini*) in collections is suggested by the fact that specimens collected alive were cryptic at and below low tide, attached to exposed, wave-swept volcanic rocks, which tend to receive far less attention from collectors than more congenial and species-rich coral reef and lagoon environments, where they have never been recorded. Institutional acronyms: ANSP, Academy of Natural Sciences, Philadelphia; AMS, Australian Museum, Sydney; BMNH, The Natural History Museum, London; LACM, Los Angeles County Museum of Natural History; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington; NMP, Natal Museum, Pietermaritzburg; USNM, National Museum of Natural History, Washington, DC.

SYSTEMATICS

Superfamily Trochoidea Rafinesque, 1815

Family Trochidae Rafinesque, 1815

Subfamily Trochinae Rafinesque, 1815

Tribe Trochini Rafinesque, 1815

Genus *Infundibulum* Montfort, 1810

Infundibulum Montfort, 1810: 167. Type species (by original designation): *Infundibulum typus* Montfort, 1810 = *Trochus concavus* Gmelin, 1791; Recent, Réunion.

Carinidea Swainson, 1840: 350. Type species (by monotypy): *Trochus concavus* Gmelin, 1791.

Description: Shell up to 54 mm in diameter, stout, base excavate, umbilicus narrow; aperture very strongly tangential, as wide as shell; periphery sharply angulate, not stellate at any stage of growth, almost flush against a flat surface. Spire sculptured with strong, close, rounded spiral cords and axial costae, intersections finely and bluntly nodular. Base weakly convex, evenly curving into narrow umbilicus, excavated from periphery. Columellar lip adapically with strong, rounded denticle, sharply retracted to insertion within umbilicus. Foot (*I. concavum*) very large, epipodium very well developed, edge finely fringed, well developed epipodial flaps beside epipodial

insertion; cephalic lappets large, papillate. Radula (*I. concavum*, figure 9) with the formula $n+5+1+5+n$, very similar to that in *Trochus* (*sensu stricto*).

Remarks: *Infundibulum* species are referable to subfamily Trochinae, tribe Trochini because of similarity to species of *Trochus* Linnaeus, 1758, and *Tectus* Montfort, 1810, in shell and radular morphology, and external anatomy. External anatomy is close to that of *Tectus fenestratus* (Gmelin, 1791) (Hickman and McLean, 1990: fig. 55b). *Infundibulum* species differ from *Trochus* and *Tectus* in the combination of low, evenly conical spire, weakly convex whorls, low sculpture, lack of peripheral nodules at any stage of growth, and widely excavated base, which fits almost flush with a flat surface. All of these character states (apomorphies) evidently enhance attachment to rocks exposed to strong wave action. *Infundibulum concavum* (Gmelin, 1791) and *I. tomlini* (Fulton, 1930) have the most strongly tangential apertures and the most widely excavated bases of any living Trochini, and they resemble limpets in ventral view when the foot is fully extended (slides of aquarium specimens of *I. concavum* provided by D. G. Herbert). Gross shell morphology strikingly parallels calyptraeid limpets of the genus *Trochita* Schumacher, 1817.

Whereas *Infundibulum* has been interpreted as a subgenus of *Trochus* by many authors, I prefer to treat *Infundibulum* as a distinct genus because of current lack of clear evidence for degrees of relatedness.

Trochus kochii Philippi, 1844, from Oman (figures 8, 10) has a similar shape and sculpture to *Infundibulum* species, but differs in having the base considerably less excavated, and a much more weakly tangential aperture (and thus presumably a more weakly expanding foot). The relationships of this species are unclear, and I refer it to *Trochus*, subgenus *Infundibulops* Pilsbry, 1889 (type species *Trochus crythracus* Brocchi, 1821) with some hesitation.

Infundibulum concavum (Gmelin, 1791)

(Figures 1–3, 9)

Trochus pyramidalis rarissimus . . . Chemnitz, 1781: 86, pl. 168, figs. 1620, 1621 (not binominal).

Trochus concavus Gmelin, 1791: 3570 (refers to Chemnitz, 1781, figs. 1620, 1621); Dillwyn, 1817: 763; Blainville, 1825: 425, pl. 32 bis, fig. 1; Wood, 1825: 134, pl. 28, fig. 7; Sganzi, 1843: 22; Philippi, 1848: 38, pl. 8, figs. 7, 8; Deshayes, 1863: 71; Fischer, 1876: 105, pl. 33, fig. 2; Kaicher, 1979: card 2087.

Infundibulum typus Montfort, 1810: 167, text fig.

Carinidea concavus: Swainson, 1840: 350.

Polydonta (*Carinidea*) *concavus*: Chenu, 1859: 357, fig. 2646

Trochus (*Polydonta*) *concavus*: Martens, 1880: 295.

Trochus (*Infundibulum*) *concavus*: Pilsbry, 1889: 40, pl. 43, fig. 13; Wenz, 1938: 311, fig. 693.

Infundibulum concavum: Cossmann, 1918: 188, text fig. 65.

Tectus concavus: Drivas and Jay, 1988, pl. 2, fig. 3.

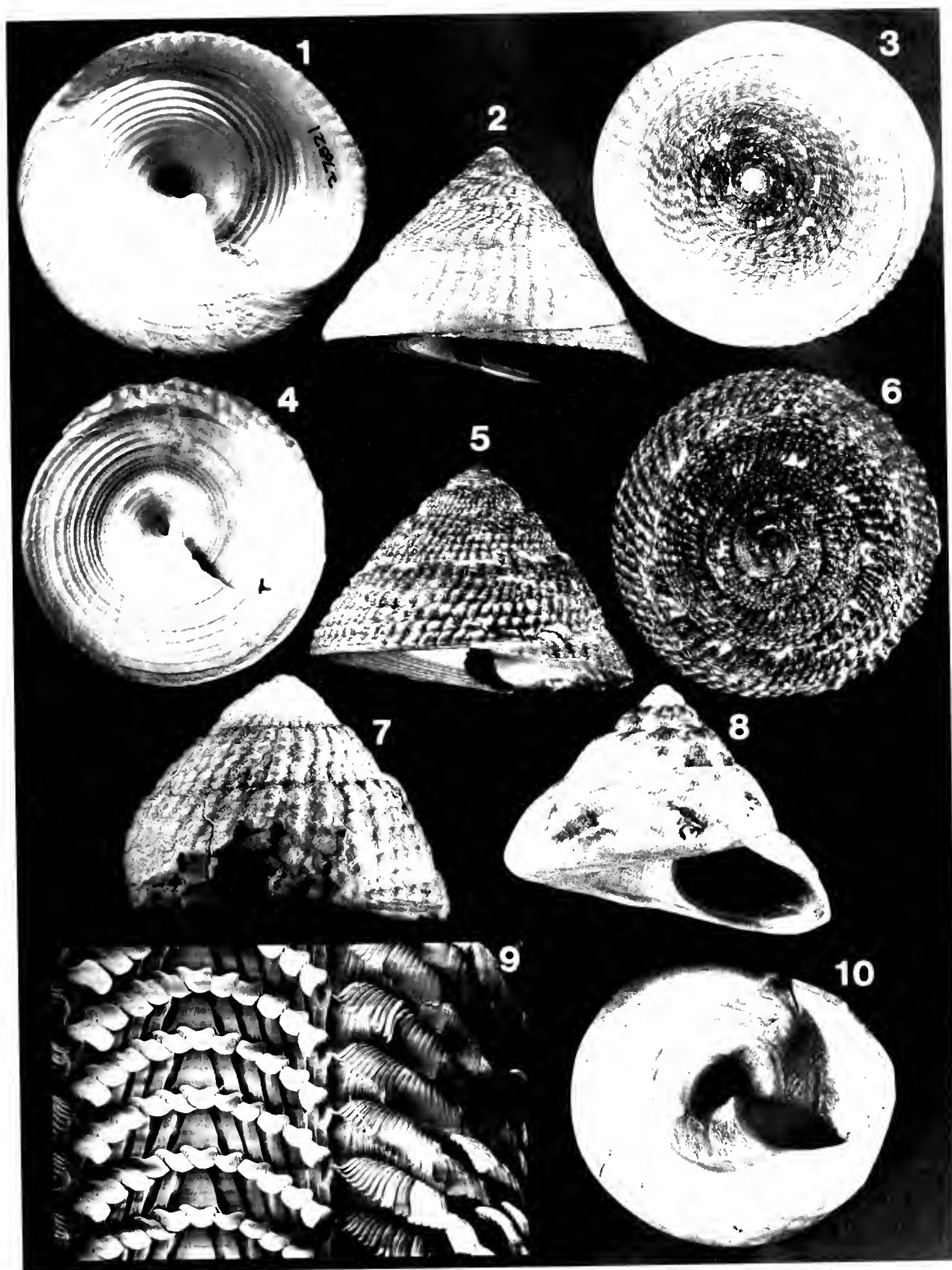
Not *Polydonta* (*Infundibulum*) *concava*: Melvill and Standen, 1895: 125 = *I. tomlini*.

Description: Shell (figures 1–3) up to 56 mm in diameter, stout, broadly conical, wider than high, weakly cyrtocoid, base excavate; aperture strongly tangential, as wide as shell; periphery sharply angulate, almost flush against a flat surface, narrow umbilicus. Spire dull green with subsutural band of irregular, dull, red and white maculations, last few whorls pinkish milky green. Base white, inner half with porcellanous glaze. Protoconch and first few teleoconch whorls unknown (eroded). Spire whorls moderately convex at first, becoming weakly convex, sculptured with low, rounded spiral cords and opisthocline, non-collabral axial costae, interspaces narrower; intersections with strong, bluntly rounded nodules; axial costae on last 2 or 3 whorls traversing rounded axial folds that are broader than the costae and tend to be more strongly opisthocline. Spiral cords 7, strong and similar on early whorls, weakening after shell attains about 8 mm diameter, obsolete on last 2 or 3 adult whorls. Excavate base convex, smoothly curving into narrow umbilicus. Outer part of base with 6 or 7 smooth, similar spiral cords, becoming obsolete on last whorl at maturity; inner (porcellanous) part of base with 6 or 7 spiral cords that become obscured by inductura at maturity. Aperture ovate. Basal lip strongly thickened, smoothly continuous with columellar lip, which is strongly thickened adapically then sharply retracted to insertion within umbilicus.

Animal (retracted, *ex ethanol*). Foot extremely large and spreading. Epipodium very well developed, edge finely fringed throughout; inner surface finely papillate, tapered macropapillae over posterior half; neck lobes convoluted, finely fringed, left lobe considerably larger and more deeply convoluted than right. Epipodial tentacles slender, narrowly tapering, 4 pairs. Epipodial flaps well-developed, bases close to epipodial insertion, edges finely fringed, 5 on right, 5 or 6 on left. Cephalic tentacles slender, narrowly tapered, subcylindrical, right tentacle base adjacent to tip of left tentacle due to oblique asymmetry of head. Eye stalks large, dorsoventrally flattened, well developed eyes in tips. Cephalic lappets well developed, edge and adjacent ventral surface

→

Figures 1–10. *Infundibulum* and *Trochus* (*Infundibulops*) species. 1–3. *I. concavum* (Gmelin, 1791), St. Paul Bay, Réunion, 56 × 40 mm (NMNZ M.270521). 4–6. *I. tomlini* (Fulton, 1930), syntype, locality unknown (possibly Western Samoa or Vanuatu), 19.0 × 26.6 mm (BMNH 1930.4.2.3). 7. *I. tomlini*, Boat Cove, Raoul Island, Kermadec Islands (Pleistocene), 25.5 × 33 (est.) mm (NMNZ M.214580); 8, 10. *Trochus* (*Infundibulops*) *kochii* (Philippi, 1844), SW coast of As Sawda, Juzor Al Halaaniyaat, Oman, 32 × 38 mm (Zoological Museum, Amsterdam). 9. Radula of *I. concavum*, north of Cap la Houssaye, St. Paul Bay, Réunion (NMP K4898).



papillate. Cephalic tentacles blackish brown, sides of foot darker, elsewhere cream.

Radula (figure 9) with the formula $n+5+1+5+n$, very similar to that in *Trochus* (*sensu stricto*) (Hickman and McLean, 1990: fig. 57D).

Type data: Holotype, the specimen illustrated by Chemnitz (1781: figs. 1620, 1621), ex Spengler collection, in Zoological Museum, Copenhagen (T. Schiøtte, pers. comm.); "kuste von Coromandel".

Material examined: North of Cap la Houssaye, St. Paul Bay, Réunion, exposed rocky shore, extreme low tide to 2 m, 24 September 1988, R. N. Kilburn and D. G. Herbert (3, NMP); St Paul Bay, Réunion, breaker zone on exposed rocky shore at low tide, M. Jay, 1994 (3 NMNZ); St Paul, Réunion, M. Jay, 1985 (3 ANSP); "Zanzibar" (8 in 3 lots, MNHN); Seychelles (4, MNHN); "Seychelles [and] Madagascar", H. Cumming collection (2, BMNH); "Madagascar(?)", M. Larrey, 1874 (1, MNHN); "Madagascar", M. Ballot (1, MNHN); "Madagascar" (1, MNHN); "Indian Ocean", H. Fischer (1, MNHN); "Indian Ocean", Staat colln (2 MNHN); "Ceylon", ex Gould colln (1 USNM); "Cochin China", M. Harmand, 1876 (2, MNHN); "Penang (?)", ex Marie and Sowerby collections (7, BMNH); "Penang" (2, LACM); "Australia", Stearns colln (1, USNM).

Distribution: Réunion and (based on Sganzin, 1843) Mauritius. Living on faces of lava rock and boulders exposed to the open sea from low tide to 2 m depth (M. Jay, pers. comm.). Records from Madagascar and the Seychelles require confirmation. Specimens in old collections reputedly from Zanzibar, Coromandel Coast, Ceylon (Sri Lanka) are of uncertain provenance, whereas Penang, Cochin China (southern Vietnam) and Australia are extremely doubtful.

Remarks: The shell of *Infundibulum concavum* is distinctive among Trochoidea in the combination of broadly conical, weakly cyrtconoid spire; flat, inwardly sloping base, conical umbilicus, and very strongly prosocline outer lip. Among trochid animals examined or that have been recorded in the literature, the external anatomy of this species seems most similar to that of *Tectus fenestratus* (Gmelin, 1791) (Hickman and McLean, 1990: fig. 55A).

Infundibulum tomlini (Fulton, 1930)
(Figures 4–7)

Polydonta (*Infundibulum*) *concava*: Melvill and Standen, 1895: 125 (not Gmelin, 1791).

Trochus (*Infundibulum*) *tomlini* Fulton, 1930: 16, pl. 3, fig. 5.

Trochus tomlini: Kaicher, 1979: card 2162.

Trochus maculatus: Marshall, 1979: 535; Marshall, 1981: 90 (not Linnaeus, 1758).

Trochus (*Infundibulum*) sp.: Brook, 1998: 256.

Description: Shell (figures 4–7) up to 36.0 mm wide, stout, broadly conical, wider than high, weakly cyrtconoid, base excavate; aperture strongly tangential, as wide

as shell, narrow umbilicus; periphery sharply angulate, not stellate, almost flush against a flat surface. Protoconch white. First 3.5 teleoconch whorls green with red spiral bands; 2 or 3 continuous median bands and 1 suprasutural band on 1st 2 whorls; spiral cords spotted and streaked with red on 3rd whorl. Subsequent spire whorls deep dull greenish or reddish grey with subsutural band of white spots or streaks. Base considerably paler than spire, inner third (approximately) porcelain-white. Protoconch 200 μ m wide, tip narrowly tapered, sculpture unknown (eroded). Teleoconch of up to 7.5 whorls. Early spire whorls moderately convex, later whorls moderately or weakly convex; sculptured with rounded spiral cords and rounded, prosocline, non-collabral axial costae, interspaces narrower; intersections with strong, bluntly rounded nodules; fine, crowded collabral growth lines throughout. Spiral cords numbering 7 per spire whorl; adapical spiral broadest in most specimens, almost fusing with adjacent spiral in some specimens; peripheral and adjacent spiral narrowest, similar; other spirals similar, peripheral spiral partly covered by succeeding whorls. Excavated base broad, weakly convex, evenly curving into narrow steep-sided umbilicus, base of which is filled with callus. Basal spirals much finer than spire spirals; outer (pigmented) part of base of most specimens with 7 or 8 weakly nodular spirals, typically 1 secondary spiral in each interspace, some interspaces in some specimens with 2 secondary spirals; 6–8 smooth spirals on inner (white) part of base, smooth, similar. Aperture ovate-trapezoidal. Columellar and basal lips smoothly continuous, thickened adapically, sharply retracted to insertion within umbilicus. Rounded spiral ridge at base of outer lip.

Animal unknown.

Type data: Originally figured syntype BMNH 1930.4.2.3 (height 19.0 mm, diameter 26.6 mm); syntype National Museum of Wales Cardiff (Trew, 1984). Fulton (1930) stated that he had seen five specimens and did not segregate a holotype. The specimens could not be localized and evidently originated from somewhere in the tropical southwest Pacific.

Other material examined: Titi Knob (Trig Sentinel), Boat Cove, Raoul Island, Kermadec Islands, cemented tuffaceous conglomerate (Pleistocene), W. R. B. Oliver (1, NMNZ); Dayrell Islet, Raoul Island, hard sandy tuff (Pleistocene), F. J. Brook, June 1991 (2, Auckland Institute and Museum); Upolu, Western Samoa, R. W. Tate (7, NMNZ); Lifou, Loyalty Islands, J. Brazier, 1873 (4, BMNH); Vanuatu, C. Bertie, 1895 (1, AMS); Erromango, Vanuatu, H. A. Robertson, 1898 (3 in 2 lots, AMS); "Red Sea", E. C. Freeman collection (3, BMNH); "Red Sea" (4, LACM); "Penang" (1, NMNZ); "Penang, ex Sowerby" (1, NMP).

Distribution: Raoul Island, Kermadec Islands (Pleistocene); Upolu, Western Samoa (record plausible because R.W. Tate collected extensively there); Aneiteum and Erromango, Vanuatu (records plausible because

there are extensive stretches of exposed rocky shore), and possibly Lifou. Specimens in old collections reputedly from the Red Sea and Penang are of extremely doubtful provenance.

Remarks: Compared with *Infundibulum concavum*, *I. tomlini* differs in attaining smaller size (maximum diameter 36.0 mm instead of 56.0 mm), in being more broadly conical, in having more strongly convex whorls, and in having much stronger axial costae and nodules on the spire, especially after the shell is about 6 mm wide. In *I. concavum* the spiral cords and nodules progressively weaken and become obsolete when the shell is 12–15 mm wide, while in *I. tomlini* the spiral cords progressively enlarge throughout.

One lot (NMP) labelled “Penang, ex Sowerby”, suggests origin from the London shell dealers Messrs. Sowerby and Fulton, who advertised *Trochus concavus* in their 1908 price list. Other “Penang” specimens of *I. concavum* and *I. tomlini* in old collections may well have originated from this source.

The Pleistocene specimens from Raoul Island (figure 7) are indistinguishable from the syntype (figures 4–6) and other Recent specimens. *I. tomlini* is absent from the Recent fauna of the Kermadec Islands (Brook and Marshall, 1998).

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On the taxonomic placement of *Unio ochraceus* Say, 1817 in the genus *Ligumia* (Bivalvia: Unionidae)

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ABSTRACT

Since 1975, the freshwater unionid mussel originally described as *Unio ochraceus* Say, 1817, has been variously assigned to the genera *Lampsilis* or *Leptodea*. The taxonomic stability of this species has been complicated by incomplete knowledge of certain features of its anatomy. Study of the mantle of this taxon leads to the conclusion that *U. ochraceus* does not belong to either *Lampsilis* or *Leptodea*. The species is assigned to the genus *Ligumia* according to established taxonomic criteria to differentiate lampsiline genera that include characters of the anatomy and larva. The mantle edge contains distinct, regular papillae along an uninterrupted, lamellate border and the glochidia are of the large type.

Additional key words: *Lampsilis*, *Leptodea*, Unionoidea, freshwater mussels, new combination.

INTRODUCTION

The unionid mussel originally described as *Unio ochraceus* Say, 1817, is discontinuously distributed east of the Appalachian divide in drainages very near the Atlantic coast of North America. The northernmost populations are found in Nova Scotia (Athearn and Clarke, 1962) and the southernmost in Georgia (Johnson, 1947).

The generic position of this species has remained an open question since Morrison (1975) and Bereza and Fuller (1975) challenged the placement of *U. ochraceus* in *Lampsilis*. The present paper attempts to resolve the issue in light of widely accepted anatomical definitions of the various genera comprising the Lampsilinae (*sensu* Heard and Guckert, 1971) or Lampsilini (*sensu* Davis and Fuller, 1981). It is proposed that the species be placed in the genus *Ligumia* and is treated as such in the remaining portion of the paper.

HISTORY OF THE PROBLEM

The question of generic allocation of this species was raised by Morrison (1975) and Bereza and Fuller (1975). Morrison's (1975) discussion was the most comprehen-

sive of the two; he argued that the taxon *Mytilus fluviatilis* Gmelin, 1791, took precedence over *Unio ochraceus* and that *M. fluviatilis*, for which he elected a neotype, belonged in *Leptodea* because of its "smaller glochidia, and a complete lack of 'mantle flaps' or papillae on the mantle margins of the females". Although his conclusion regarding the generic placement of *U. ochraceus* has been widely adopted, his argument for *M. fluviatilis* has not gained acceptance. One major issue regarding the position of *L. ochraceus* concerns the lack of the "mantle flap" (Morrison, 1975), a character included in the prevailing definition of *Lampsilis* (*sensu stricto*), the genus to which the species has been assigned by many authors (e.g., Ortmann, 1919; Reardon, 1929; Johnson, 1947, 1970; Burch, 1973). Ortmann (1912) reassessed the characters defining lampsiline genera. This author used primarily anatomical and larval characters in the diagnosis of the various genera, including: (1) features of the mantle margin anterior to the inhalant aperture, (2) the size and shape of the glochidia, (3) the nature of the marsupial portion of the female gill (four "types"), and (4) the degree of attachment of the inner gill to the abdomen. Ortmann (1912) defined the mantle flap, a feature of *Lampsilis*, as a highly pigmented free lobe extending from the mantle margin anterior to the inhalant aperture with a "lacerated appearance." Papillae are not present in this region of the mantle. The mantle flap is best represented in the female, reduced in the male.

Ortmann (1912) was apparently unable to examine anatomical material of *Ligumia ochraceus* and consequently omitted the species in his discussion. Later, Ortmann (1919), still unfamiliar with the anatomy, placed the species in *Lampsilis*, presumably on the basis of shell characters. Subsequent study (Bereza and Fuller, 1975; Morrison, 1975; Kat, 1983; Smith, 1995) has shown that *Ligumia ochraceus* clearly does not possess a mantle flap. Nevertheless, *L. ochraceus* continued to be included in *Lampsilis*, at least provisionally, by several investigators (Fuller, 1977; Johnson, 1980; Clarke, 1981a; Kat, 1983; Porter, 1985; Strayer, 1987). Certainly part of the reason

for maintaining *L. ochracea* in *Lampsilis* has been the strong resemblance of its shell to other species of *Lampsilis sensu stricto* and conservatism in the absence of a definitive description of the species.

Otherwise, following the suggestion of Morrison (1975), the species has been placed within *Leptodea* (D. Stansberry, in Porter, 1985; Smith, 1991; Stiven and Alderman, 1992; Strayer and Jirka, 1997; Turgeon *et al.*, 1998). Ortmann (1912) stated that the mantle margin of *Paraptera* (= *Leptodea*), based on the type, *L. fragilis*, was lamellate with at most marginal crenulations, but without papillae or a flap. There were little or no observed differences between the sexes. The glochidia were described as "very small" and "suboval."

Descriptions of the mantle of *Ligumia ochracea* from North Carolina and Nova Scotia (Porter, 1985, and Kat, 1983, respectively) have clearly shown, in conjunction with characters discussed below, that *L. ochracea* does not belong within *Leptodea* either. Porter (1985) noticed in his study of this species the occurrence of some papillae along the margin of the mantle of females and males. Whereas Lea (1863), Reardon (1929), Bereza and Fuller (1975) and Morrison (1975) did not report these papillae, Kat (1983) mentioned observing a few papillae.

At various junctures, and with apparent awareness of the difficulties regarding the placement of *Ligumia ochracea*, both Fuller (1977) and Clarke (in Porter, 1985) indicated that a new genus name was forthcoming. To date, however, no such name has been published.

MATERIALS AND METHODS

Material cited in the discussion of *Ligumia ochracea* is cataloged in the Museum of Zoology, Invertebrate Division, University of Massachusetts at Amherst. The catalog numbers are as follows:

Leptodea fragilis (Rafinesque, 1820) UMA MO. 1270, 1381, 1383, Vermont;

Ligumia nasuta (Say, 1817) UMA MO. 769, 832, 1129, 1810, 1849, 1904, Connecticut, Massachusetts, New York;

Ligumia ochracea (Say, 1817) UMA MO. 1053, 1234, 1241, 1809, 1822, 1823, 1850 Connecticut, Maine, Massachusetts, and North Carolina;

Ligumia recta (Lamarck, 1819) UMA MO. 1137, 1379, 1902, Vermont, New York;

Ligumia subrostrata (Say, 1831) UMA MO. 1903, Illinois.

Specific localities will be furnished upon request.

All specimens used in this study were prepared following the method described by Smith (1996). For histological studies, a portion of the mantle edge measuring approximately 5 mm² was excised, cleared, and infiltrated with paraplast[®]. Embedded specimens were sectioned at 5 μ m intervals and stained with hematoxylin and eosin. Bright field micrography was accomplished with a Wild M20 microscope. Glochidia were either whole mounted on slides or mounted on Cambridge SEM stubs and sputter-coated with gold. SEM micrography used a JEOL JSM-5200 scanning electron microscope.

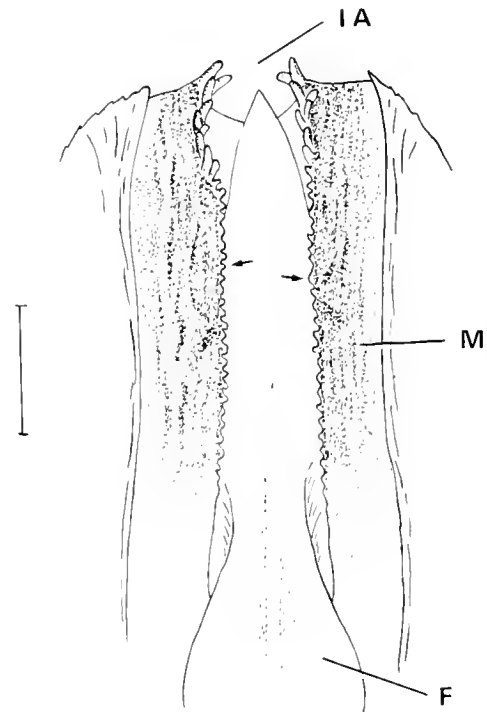


Figure 1. Mantle region of an adult female *Ligumia ochracea* posterior to the foot. Arrows denote papillae along inner margin. F = foot, IA = inhalant aperture, M = mantle. Scale line = 15 mm.

RESULTS

Close examination of the mantle margin of carefully relaxed preserved male and female specimens of *L. ochracea* revealed a row of small but regular papillae extending along the mantle margin from the base of the inhalant aperture anteriorly to the gape of the foot. The papillae are regularly arranged (figure 1), rather closely set, and average about 100 μ m in length (figures 2, 3). They are less developed than those of *Ligumia nasuta*, *L. subrostrata*, or *L. recta*, which may reach >1 mm in length. The mantle edge bearing these papillae is slightly lamellate and there is no indication of a flap or lacerations, as is also the case with *L. nasuta*, *L. subrostrata*, and *L. recta*. The papillae of *L. ochracea* appear at a young age, about two years as evidenced by prominent growth marks on shells of 20–25 mm in length. At this age (shell size), the papillae are not as closely set as in the adult and there is no evidence of crenulation, a flap, or a "lacerated" structure (*sensu* Ortmann, 1912).

The mantle edge of *L. ochracea* is pigmented with a cream, orange-ochre, or light-grey background and variegated with darker grey. Although most of the darker pigment is distributed near the posterior portion of the mantle edge (figure 1), no specific pattern is evident. In this regard, *L. ochracea* is intermediate between *L. nasuta*, which has very dark pigment throughout and a discernible pattern, and *L. recta* and *L. subrostrata*, in

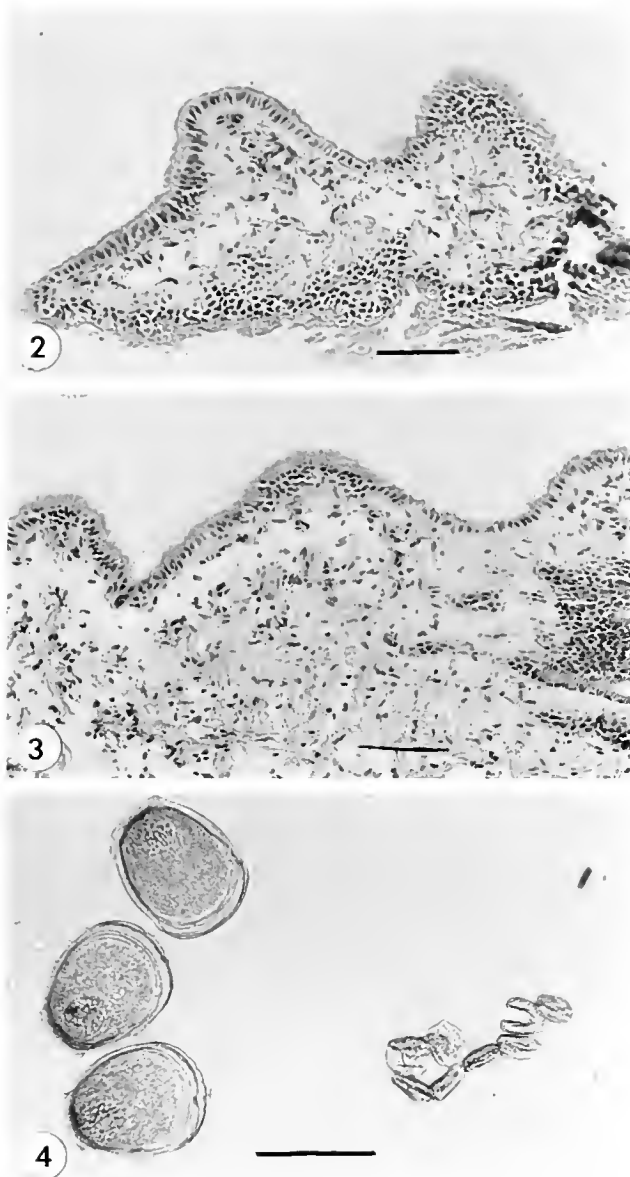


Figure 2. Section of mantle edge of female *Ligumia ochracea* (shell length = 55 mm) from the Connecticut River, Connecticut. Scale line = 50 μ m.

Figure 3. Same as figure 2, different specimen (shell length = 72 mm). Scale line = 50 μ m.

Figure 4. Glochidia of *Ligumia ochracea* (left) and *Leptodea fragilis* (right). Scale line = 200 μ m.

which the mantle edge is a slightly variegated, patternless, light- to dark-gray. The mantle margins of *Ligumia subrostrata* and *L. recta* differ in that the inner edge of the mantle of *L. subrostrata* has a very dark-brown border, a feature absent in *L. recta*. Both species possess a densely pigmented "eye spot" at the base of the inhalant aperture. In *L. recta*, the spot is small and not swollen; in *L. subrostrata*, however, the spot is actually a slightly thickened pad, almost lobe-like in a few specimens. The

function of these spots is as yet unclear, although it is supposed that they act as some sort of light receptor. No such spots are apparent externally in either *L. nasuta* or *L. ochracea*.

Examined specimens of *Leptodea fragilis* comply with Ortmann's (1912) diagnosis for the most part. In one female, a few small papillae extend slightly anteriorly from the inhalant apertural papillae but subsequently disappear completely. In the remaining specimens, no extra-apertural papillae are evident. The crenulation reported by Ortmann (1912) is actually no more than a slight sinuation of the margin, the edge being uninterrupted whatsoever for the length of the mantle. The mantle margin is slightly more lamellate in the female than in the male, but there is little difference between the sexes. Although the specimens have been in alcohol for several years, there is no indication of concentration of pigment in the posterior region of the mantle, and no specific pattern was observed during the original preparation of the specimens (D. G. Smith, unpublished observations).

The glochidia of *L. ochracea* are over twice the size of those of *Leptodea fragilis* (figure 4) (see also Porter, 1985). The glochidia of *L. fragilis* from Vermont measure on the average 73 μ m (length) by 94 μ m (height) and possess a narrow hinge. This compares well with observations on glochidia of this species by Surber (1912). Glochidia of *L. ochracea* from Massachusetts have a mean length of 222 μ m and a mean height of 287 μ m (see Porter and Horn, 1980, for similar values of North Carolina populations). These values are: slightly smaller than those for glochidia from *L. nasuta* from Massachusetts and New York, which have a combined mean length of 256 μ m and mean height of 318 μ m; slightly larger than *L. subrostrata* with a mean length of 205 μ m and mean height of 261 μ m; and nearest to values reported for *L. recta*, with mean values of 220 μ m by 270 μ m (Ortmann, 1912; Baker, 1928). The ratio of glochidia length:height among the species is rather consistent, 0.77 for *Ligumia ochracea*, 0.78 for *L. recta* and *L. subrostrata*, and 0.80 for *L. nasuta*. The ratio of glochidial length:height in *Leptodea fragilis* is similar, 0.78, however, as noted above, the glochidia of this species are less than one third the size of *Ligumia ochracea*. The glochidia of *L. ochracea* (figure 5) are most similar to those of *L. subrostrata*, which also has a narrow hinge; those of *L. nasuta* (figure 7) possess a wider hinge. The surfaces of the glochidial shell of each species are provided with minute pores less than 5 μ m in diameter (figures 6, 8) and the margin opposite the hinge is evenly curved and smooth.

DISCUSSION

As concluded earlier by Bereza and Fuller (1975), *Ligumia ochracea* can not be assigned to either *Lampsilis* or *Leptodea* as these genera are currently defined. In the case of *Lampsilis*, this is further supported by studies using biochemical techniques (Kat, 1983; Stiven and Al-

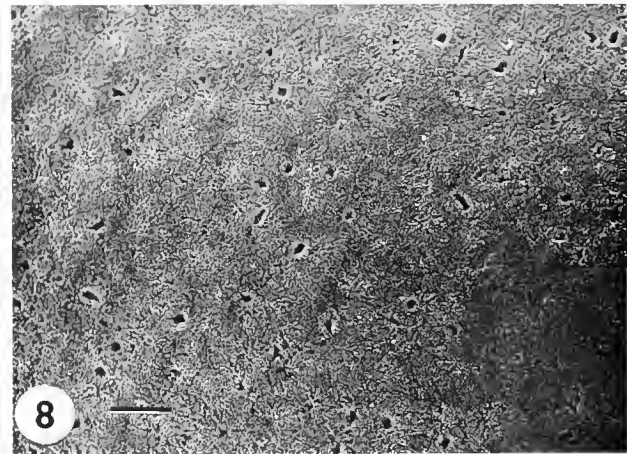
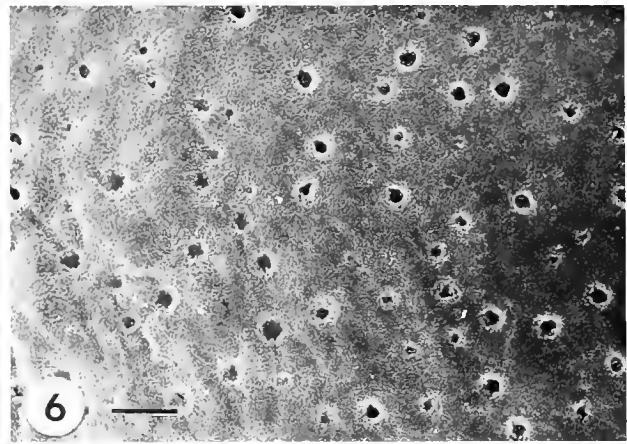
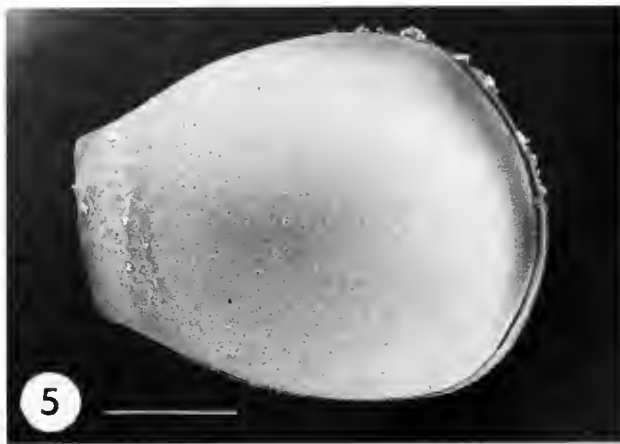


Figure 5. Glochidium of *Ligumia ochracea*. Scale line = 100 μm . **Figure 6.** Enlargement of glochidial shell surface of *Ligumia ochracea*. Scale line = 10 μm . **Figure 7.** Glochidium of *Ligumia nasuta*. Scale line = 100 μm . **Figure 8.** Enlargement of glochidial shell surface of *Ligumia nasuta*. Scale line = 10 μm .

derman, 1992), which have shown that *Ligumia ochracea* is quite distantly related to two sympatric species of *Lampsilis* with mantle flaps. The only recognized lampsiline genus to which the species *ochracea* can be allocated is *Ligumia*. In review, Ortmann (1912), defined a large genus, *Eurynia*, which was distinguished from other lampsiline genera principally by the presence of papillae, variously developed, along the mantle margin and evident in both the male and female. Glochidia of *Eurynia* species were listed as "subovate, of medium size, or rather large." Other characters, including the nature of the marsupial gill (Ortmann "type 4") and degree of attachment of the inner gill were essentially as in *Lampsilis*. The three subgenera of *Eurynia* listed by Ortmann (1912) [*Micromya*, *Carunculina*, *Eurynia*] were eventually raised to genus rank and their nomenclature stabilized (Ortmann and Walker, 1922). The nominotypical genus *sensu* Ortmann (1912) is *Ligumia* Swainson, 1840 [type-species: *Unio recta* Lamarck, 1819] and is defined (Ortmann, 1912, as subgenus *Eurynia*) by having "quite regular, uniform, smaller or larger papillae, reaching about the middle of the lower margin." *Ligumia ochra-*

cea fits this description and, though less developed, its papillae are similar in their external gross morphology to those of *L. nasuta*, less so to *L. recta*, in which the papillae are somewhat crowded and slightly irregular.

At present, erection of a new genus for this species seems unwarranted, in the absence of urgently needed critical anatomical studies of the various nominal lampsiline genera.

ACKNOWLEDGMENTS

I thank Richard L. Johnson whom, though not in complete agreement with some of what has been presented, provided useful comments on an earlier draft of this article. David Strayer, Catherine Corey, Kevin Cummings, Ethan Nedeau, and Sarah Riseman donated many specimens used in this study. The study was funded in part by a grant from The Nature Conservancy, Connecticut Chapter.

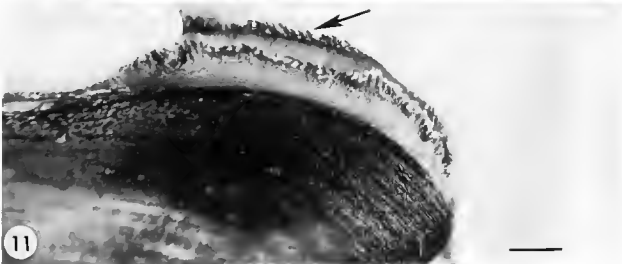
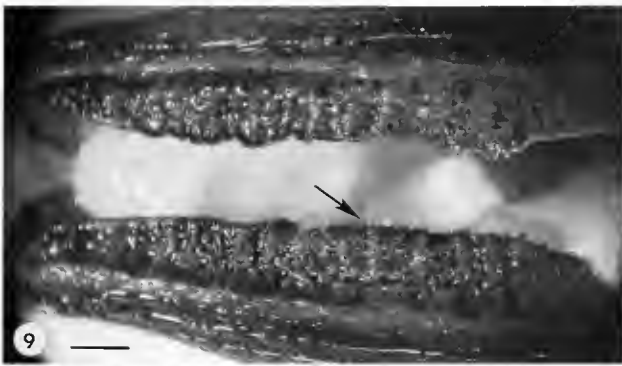


Figure 9. Mantle margin of female *Ligumia nasuta*. Arrow denotes papilla. Scale line = 5 mm.

Figure 10. Mantle margin of female *Ligumia subrostrata*. Arrow denotes papilla. Scale line = 5 mm.

Figure 11. Mantle margin of female *Ligumia recta*. Arrow denotes papilla. Scale line = 5 mm.

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Latirus beckyae, a new species of Fasciolaridae (Neogastropoda) from Brazil

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ABSTRACT

Latirus beckyae new species is described from off Vitória, Espírito Santo State, and off Santos, São Paulo State, Brazil. The new species is readily distinguished from conchologically similar species in the same genus by its caramel color, white spiral banding, and angular profile.

Additional key words: Southwestern Atlantic Ocean, southeastern Brazil, Peristerniinae.

INTRODUCTION

In May, 1994, local shrimpers trawling in 30–35 m off Vitória, Espírito Santo State, and in 190 m off Santos, São Paulo, Brazil, collected specimens of *Latirus* that were tentatively identified as *Latirus cf. varai* Bullock, 1970. Although superficially similar to *L. varai*, these specimens are readily distinguished from all other species of western Atlantic *Latirus*. Despite having been collected alive, no soft parts of the new species were available for study, and the species is herein described solely on the basis of shell morphology. Institutional abbreviations are as follows: ANSP, The Academy of Natural Sciences, Philadelphia; IBUFRJ, Instituto de Biologia, Universidade Federal do Rio Janeiro, Brazil; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MORG, Museu Oceanográfico, Fundação Universidade do Rio Grande, Brazil; UNSM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Fasciolaridae Gray, 1853

Subfamily Peristerniinae Tryon, 1880

Genus *Latirus* Montfort, 1810

Type species: *Latirus aurantiacus* Montfort, 1810, by monotypy [= *L. gibbulus* (Gmelin, 1791)].

Latirus beckyae new species
(Figures 1, 2)

Description: Shell length to 54 mm. Shell broadly fusiform, biconic, moderately heavy, with prominent axial and spiral sculpture. Protoconch with 1 3/4–2 smooth,

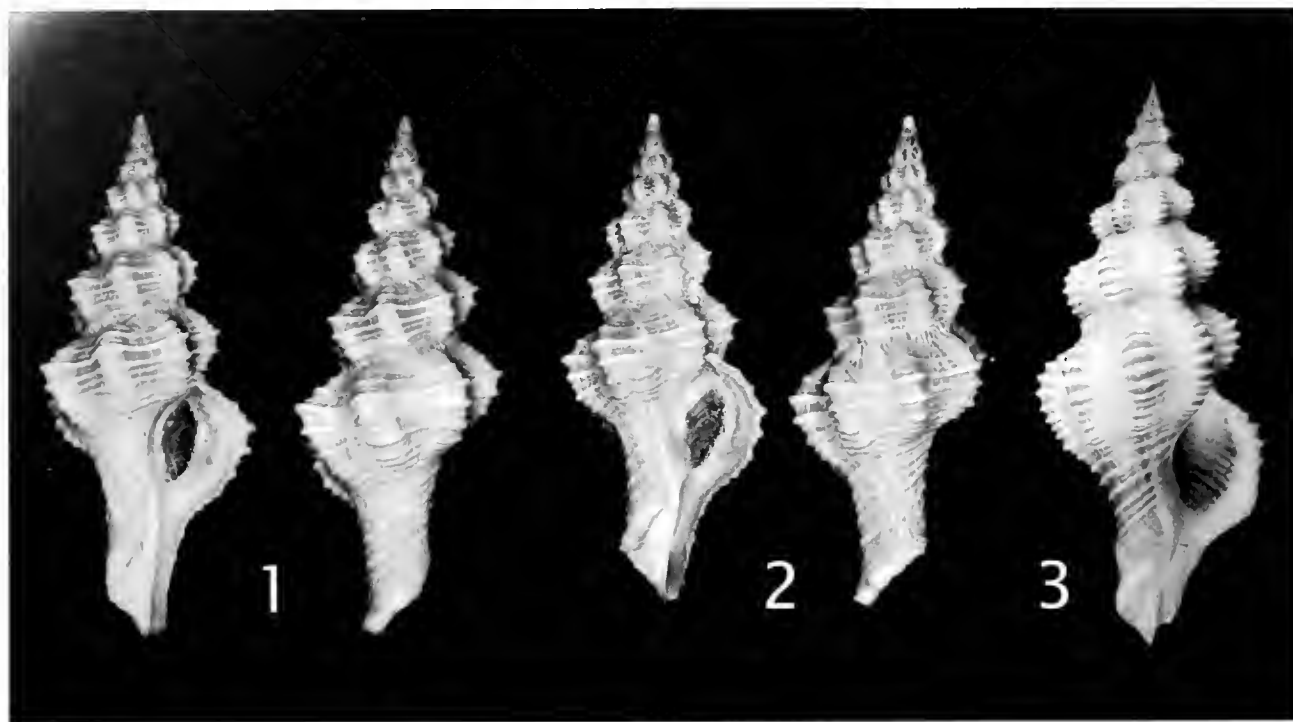
bulbous, white, translucent whorls, with axial sculpture and shoulder developing in last 1/4 whorl. Transition to teleoconch abrupt, distinguished by coarser axial sculpture, onset of spiral sculpture, and by change of color from white to orange-tan. Teleoconch with up to 8 1/2 convex, strongly sculptured whorls. Axial sculpture dominant, consisting of 7–8 strong, broad ribs per whorl, aligned with spaces between ribs of previous whorl. Ribs rounded on early whorls, becoming increasingly angular with size. Growth lines forming widely spaced lamellae, eroded on early whorls and on spiral cords, most prominent along adpressed suture and between spiral cords on body whorl. Spiral sculpture of strong, cream-colored cords (3–5 on early whorls, 5–7 between suture and periphery, 6–7 between periphery and siphonal canal, 6–9 on siphonal canal) that are most pronounced along axial ribs. Weak threads (1–2) may be present between adjacent cords. Aperture ovate, with weakly developed posterior canal. Columella with 1 weak, narrow fold below mid-aperture, and one weak, broad fold over the fasciole, which may represent two partially fused folds. Outer lip crenulated, with 12–15 irregular lirae running into the aperture. Siphonal fasciole well developed. Pseudumbilicus slit-like, prominent, open. Siphonal canal as long as aperture, broad, open, proximal end demarcated by tubercles on columella and outer lip. Shell color a dense caramel-tan, with cream spiral cords and threads. Operculum medium dark-brown, claw-like, with terminal nucleus. Periostracum unknown.

Type locality: Off Vitória, Espírito Santo State, Brazil, in 30–50 m.

Type material: Holotype, USNM 880231 (51.3 mm); Paratype 1, USNM 880232 (48.8 mm); Paratypes 2–3, Snyder Collection (43.2 mm and 53.4 mm); Paratypes 4–5, IBUFRJ 9121 (55.3 and 51.2 mm); Paratype 6, MORG 39008 (50.4 mm); Paratype 7, MNRJ 7696 (52.3 mm), all from the type locality. Paratype 8, ANSP (52.7 mm), off Santos, São Paulo State, Brazil, in 190 m.

Etymology: The species is named for the author's eldest daughter, Becky.

Discussion: *Latirus beckyae* resembles *L. varai* (figure 3; see also Bullock, 1970) but is readily distinguished



Figures 1–2. *Latirus beckyae* new species **1.** Holotype, USNM 880231 (51.3 mm), **2.** Paratype 1, USNM 880232 (48.8 mm), both from off Vitoria, Espírito Santo State, Brazil, in 30–50 m.

Figure 3. *Latirus varai* Bullock, 1970. Holotype, MCZ 262589 (70.0 mm), from Off Gibara, Oriente Province, Cuba, in 183 m.

from it by its smaller, differently colored shell. *Latirus beckyae* has roughly half as many strong spiral cords as *L. varai*. The axial ribs in *L. beckyae* are whitish whereas in *L. varai* the axial ribs are light chestnut brown. Larger (80+ mm), whitish specimens of *Latirus* have recently been taken off San Salvador, Bahamas, in depths of 490 m by research submersibles (D. Dan, pers. comm.). These closely resemble *L. varai*, but have far fewer spiral cords (R. Bullock, pers. comm.). Not enough material is presently available to determine whether these specimens represent a deep-water form of *L. varai* or another new species of deep-water *Latirus*. *Latirus beckyae* is easily differentiated from the San Salvador specimens by its smaller size, darker color, and coarser, more prominent sculpture.

Latirus beckyae might also be confused with some specimens of *Latirus cuna* Petuch, 1990, from Honduras and east Panama (Petuch, 1990). This latter species is usually bright orange or yellow and broader overall with a proportionally shorter canal than *L. beckyae*. *Latirus cuna* has pairs of white cords on the body whorl and sometimes on earlier whorls as well as on the terminal part of the body whorl. Because of these white spiral cords, an orange-brown color form of *L. cuna* superficially resembles *L. beckyae*. Separation of the two species is easy: *L. beckyae* is more elongate and angular, with a relatively larger teleoconch than *L. cuna*.

There are four previously known species of *Latirus* endemic to Brazil, all of which are very distinct from *Latirus beckyae*. *Latirus devyanae* Rios, Costa and Cal-

vo, 1994, from southeastern Brazil, has a distinctive curved siphonal canal and grows to just 35 mm (Rios, Costa and Calvo, 1994). *Latirus lacteum* Matthews-Cascon, Matthews and Rocha, 1991, from northern Brazil, is glossy-white and grows to just 32 mm (Matthews-Cascon, Matthews and Rocha, 1991). *Latirus ogum* Petuch, 1979 (Petuch, 1979; Rios, 1994: pl. 42, fig. 574), from eastern Brazil has few large smooth axial nodules and attains 43 mm. *Latirus vermeiji* Petuch, 1986, from the northern coast of Brazil, is very small with a short stumpy canal, growing to just 26 mm (see Petuch, 1986).

There are five other Caribbean species of *Latirus* also found in northern Brazil. Four of them differ in shape and color from *Latirus beckyae*: *Latirus carinifer* (Lamarck, 1822), (Rios, 1994: pl. 42, fig. 572), *Latirus angulatus* (Röding, 1798) (Rios, 1994: pl. 42, fig. 572), *Latirus infundibulum* (Gmelin, 1791) (not Rios, 1994: pl. 42, fig. 573; see Abbott, 1974: color pl. 11, fig. 2491), and *Latirus virginensis* Abbott, 1958 (Rios, 1994: pl. 42, fig. 575). *Latirus bernaensis* Bullock, 1974, is uniformly light-cream-orange, a color that sets it apart from *Latirus beckyae* (see Bullock, 1974).

There are six species of *Fusinus* known from Brazil, of which two are superficially similar to *Latirus beckyae*. The other four species that cannot possibly be confused with *L. beckyae* are large *Fusinus*, all with more or less dark brown markings. These are *Fusinus brasiliensis* (Grabau, 1904) (Rios, 1994: pl. 42, fig. 566), *F. closter* (Philippi, 1850) (Rios, 1994: pl. 42, fig. 567), *F. marmoratus* (Philippi, 1846) (Rios, 1994: pl. 42, fig. 569),

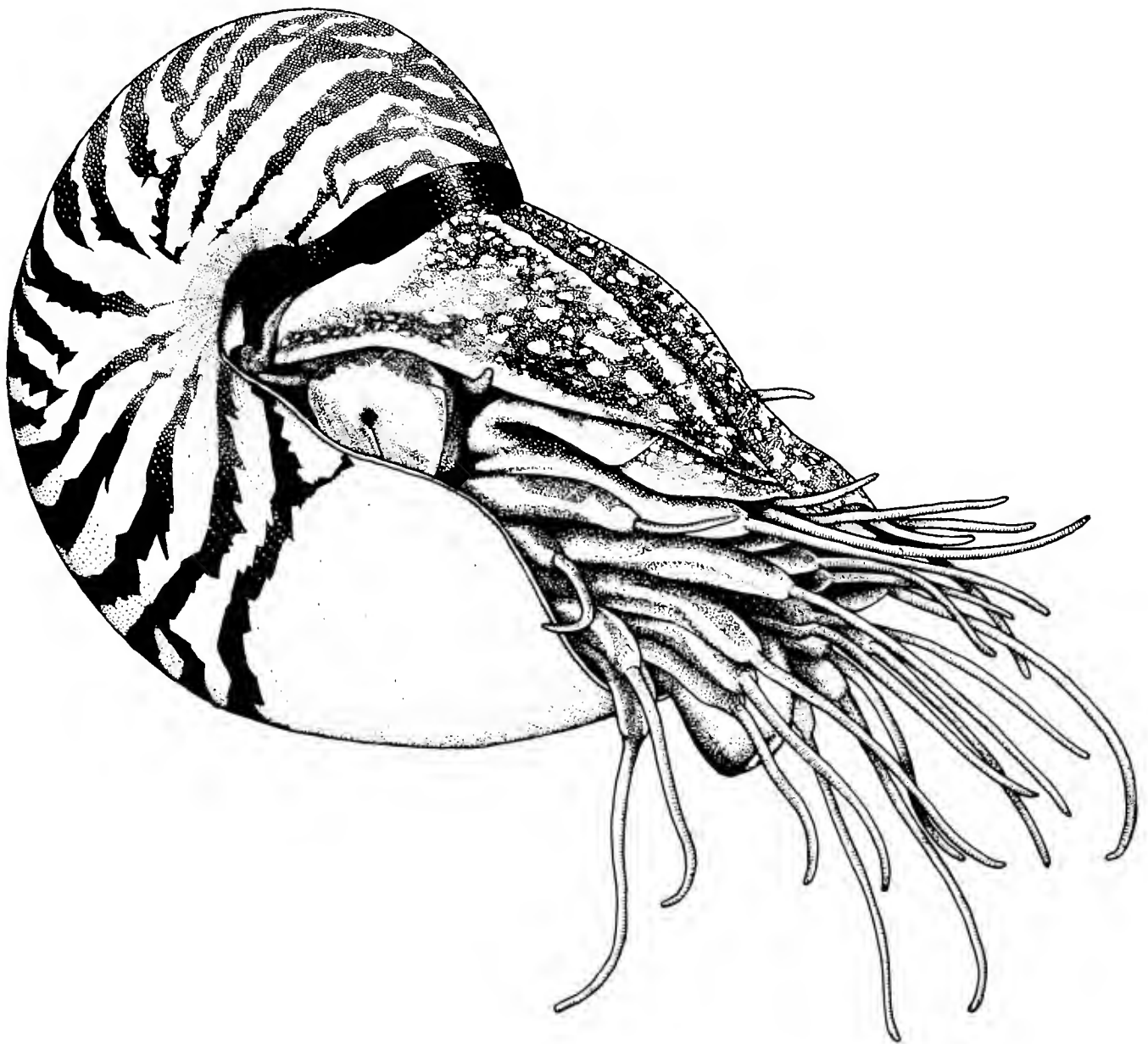
and *E. strigatus* (Philippi, 1850) (Rios, 1994: pl. 42, fig. 570). The superficially similar species are *Fusinus hartvigii* (Shuttleworth, 1856) (Abbott, 1974: color pl. 11, fig. 2494) and *Fusinus frenguelli* (Carcelles, 1953) (Rios, 1994: pl. 42, fig. 568). *Fusinus hartvigii*, a species erroneously placed in *Latirus* by Kaicher (1978: card 1816), exhibits a different color pattern and more numerous axial ribs than *Latirus beckyae*. (*Fusinus paeteli* (Dunker, 1867) is a synonym of *F. hartvigii* named from Brazilian material.) Finally, young specimens of *Fusinus frenguelli* could be confused with *Latirus beckyae* (the species was originally named in the genus *Lathyrus* [= *Latirus*]). The axial ribs of this species are more numerous and its coloration ranges from uniform white to pale orange.

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